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SOCIAL ORGANIZATION AND BEHAVIOUR OF MUSKOXEN (*OVIBOS MOSCHATUS*) ON BATHURST ISLAND, N.W.T.

by

© DAVID ROBERT GRAY

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF ZOOLOGY

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Social Organization and Behaviour of Muskoxen (Ovibos moschatus) on Bathurst Island, N.W.T." submitted by David Robert Gray in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

The social organization and behaviour of a free-living high arctic population of muskoxen (*Ovibos moschatus*) was studied during summer and winter. The study population size was lowest in early summer and rose to about 100 in early winter. Limited resightings of tagged muskoxen suggest frequent movements between the study area and other grazing areas on the island. Few solitary bulls and no calves or yearlings were observed between May 1968 and May 1970. Sex ratios in herds approximated equality and few single-sex herds were seen.

The activity cycle for muskoxen consisted of alternating periods of feeding and resting-rumination of about 150 minutes duration. Activity within most herds was synchronized but large winter aggregations did not show this same synchrony. Some animals remained together as a single herd or part of several different herds for up to three months. Other herds were less stable with much mixing, joining and splitting of herds occurring. During most daily feeding movements leadership was not evident but certain individuals did influence other herd movements.

Grooming and drinking were infrequent. Feeding behaviour in winter was variable, depending on snow conditions, but usually consisted of removing snow cover by pawing. In winter herds grazed in broad valleys rather than on wind-swept hillsides. No evidence of grouping during winter storms was

noted.

A linear dominance hierarchy was present among the bulls of herds studied intensively. Displacements from winter feeding craters and the initiation and outcome of butting and charging interactions were closely related to the dominance position of the individuals. Broadside displays and gland-rubbing displays were usually performed by dominant bulls. The dominant bull acted as herd leader in situations of disturbance and during some herd movements. Joining of two herds occurred with no overt interactions, after dominance or threat displays by a dominant bull or after a clashing fight between two dominant bulls. Behaviour patterns seen during between-herd interactions also occurred in interactions with caribou, humans and attacking wolves. Behaviour patterns apparently unique to the muskox are the rubbing of the preorbital gland against the foreleg and the pressing together into a line or rough circle as a defence against predators.

During the expected rutting season, no copulations were seen. Muskox bulls performed sniffing, lip-curling and fore-leg kicking and only rarely, mounting behaviours. Many courtship behaviours were performed by dominant bulls. Cows did not appear receptive. The sex ratio in herds remained the same and no harem-formation or tending-bond behaviour was observed. An increase in completeness of courtship behaviour and the presence of calves in 1971 indicate a return to a breeding condition in the population.

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This study began while I was employed as a field assistant by the National Museum of Natural Sciences, Ottawa, in the summer of 1968. From 1969 to 1971 the Canadian Wildlife Service provided financial support (contracts No. 6970-0021 and No. WE 70-71-4) while the N.M.N.S., in conjunction with the Polar Continental Shelf Project (Department of Energy, Mines and Resources), continued to provide logistic support including accommodation at the N.M.N.S. High Arctic Research Station, food, ground transportation, and air transport from Resolute Bay to Bathurst Island.

Further financial support was provided through the Boreal Institute for Northern Studies and the Department of Zoology, University of Alberta, and through National Research Council funds (NRC grant A-3499) awarded to my academic supervisor, Dr. A. L. Steiner.

King Resources Company and Sun Oil Company kindly provided some flying time for muskox surveys and, during the 1970-71 winter, Sun Oil Company provided several trips to our camp to deliver late-arriving equipment and to drop mail during the "dark" period.

I would like to thank each of the above organizations for their interest in and support of this project.

In a research project of this nature, many persons have helped in a variety of ways and it is difficult to thank each of them individually. I would however like to especially acknowledge the assistance given by Dr. F. Roots and Mr. E. Chapman of P.C.S.P., the P.C.S.P. crew at Resolute Bay and the pilots of the several air charter companies who serviced our camp.

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INTRODUCTION

The range of the muskox (*Ovibos moschatus*) is remote and, until recently, seldom visited by biologists. Consequently, the muskox is one of North America's least known ungulates. Information on the behaviour and ecology of the species is minimal and its taxonomic relationship to other ungulates is poorly understood.

Several recent developments in Canada's north have made the need for greater biological knowledge more pressing. The initial success of domestication projects in several circumpolar areas (Wilkinson, 1971), the possibility of sports hunting of muskoxen (Lent, 1971), and the intense activity connected with exploration and exploitation of the non-renewable resources over the range of muskoxen, all require new and detailed information on all aspects of muskox biology.

In an attempt to expand our knowledge of the biology of this species, this study of the behaviour of the white-faced muskoxen (*O. m. wardi* Lydekker) was initiated by the National Museum of Natural Sciences in the summer of 1968 and continued in conjunction with the Canadian Wildlife Service and the University of Alberta.

There is a great deal of popular and semi-scientific literature dealing with the natural history of muskoxen. The early explorers of Canada's arctic regions were well aware of some aspects of muskox behaviour since they often depended on these animals for food. An extensive review of muskox biology, based on these early accounts, was compiled by Hone in 1934. Although much useful and interesting information was recorded by these early writers, many observations are inaccurate and result in a general distrust of much anecdotal information.

The first long term studies of muskox biology were carried on in Greenland by Pedersen (1958, 1962) and Vibe (1958, 1967). In Canada most investigations were limited to short reports on numbers, feeding habits, etc. (eg., Bruggemann, 1953, 1954; MacDonald, 1954). The Canadian Wildlife Service, in 1951, initiated a long term muskox research project under J. S. Tener, which concentrated on ecology and taxonomy (Tener, 1958, 1960, 1965). His co-worker described the history, ecology and distribution of the muskox (Harington, 1961).

Both authors dealt with natural history and behaviour and reviewed the existing literature. However, it is sometimes difficult to determine which information was based on their own observations and which was accepted as

general "knowledge" of muskox biology.

From the end of Tener's research program in 1961 to the initiation of the present study, little research was conducted on wild muskoxen. Freeman (1970, 1971) compiled information on the productivity of certain Canadian muskox populations and a long term study of the productivity of muskoxen on Devon Island, N.W.T., is underway at present (Hubert, 1972).

Animals held in captivity in Alaska for domestication projects have provided some additional information on muskox behaviour (Teal, 1959; Wilkinson, 1971). Lent (1970) investigated some aspects of maternal behaviour in these Alaskan muskoxen. Herds transplanted to Nunivak Island in Alaska have been studied intensively in recent years (Bos, 1967; Spencer and Lensink, 1970; Lent and Knutson, 1971).

The study I undertook is the first long term investigation of a localized population of wild muskoxen. The 22 months of field work have extended over a four-year period and have covered all months of the year.

The original and primary purpose of this study was to record and describe the total behavioural "repertoire" of the muskox. Initially, emphasis was to be placed on social behaviour, especially maternal and rutting behaviour. As it

became evident that maternal behaviour was totally absent in the study population and that rutting behaviour was observed far less frequently than expected, a broader approach was taken in an attempt to understand and explain the observed situation and to establish a necessary baseline for further studies. The secondary aim of this study thus became to clarify the relationships between behaviour, social organization and the environment.

It was also hoped that this study would provide further information on the taxonomic relationships between muskoxen and related ungulates through comparison of behaviour patterns.

DESCRIPTION OF THE SPECIES

Tener (1965) reviewed what is known of the general morphology of the muskox. Some features which are particularly important in view of their relation to certain behavioural patterns discussed later are briefly described here.

Sexual dimorphism of adults is expressed in relative body size and, more obviously, in horn size, shape, and development. Horns of the adult female are slender and separated at the middle of the forehead by a patch of whitish wool which is usually long enough to hide the horn bases entirely. Horns of adult males are massive in comparison --

thicker and more outward curving and meeting at the midline (Figure 1). Only during the height of shedding does any wool cover part of the horn bases. Allen (1913) gives the average weight of 23 adult female skulls from Greenland as 7 lb (3.2 kg) and the average weight of 29 adult male skulls from the same area as 18 lb (8.2 kg). The horns of older males are darker and have more cracks than those of younger males.

Both sexes have a mane of hair and wool extending from the neck just below the lowest curve of the horn up to the top of the shoulder hump.

The colour of the pelage is generally very dark brown to black with the exception of a saddle-shaped area on the back behind the shoulder hump, the area around the muzzle, the area between the horns of females and subadult males, and the lower part of the legs (Figure 1). These areas are all creamy-white in colour.

According to Pocock (1910), muskoxen do not have pedal glands. Pedersen (1958), however, states that an interdigital organ is found in both sexes on all four extremities. Sack and Ballantyne (1965) did not report on this aspect of structure in their anatomical examination of a muskox calf.

Preorbital glands are present in both sexes. The

Figure 1. Adult bull (left) and adult cow muskox

pear-shaped gland is surrounded by a capsule of connective tissue and lies on the flat lacrymal bone just in front of the orbit (Figure 2a). One gland from an adult male measured 4.5 x 4 x 2 cm. with the cutaneous hair-filled tube (described by Sack and Ballantyne, 1965) extending the length of the gland (Figure 2b). My own preliminary histological examination indicated that the gland is of the sudoriferous apocrine type with extensive sebaceous glands associated with the hair follicles.

DESCRIPTION OF THE STUDY AREA

Bathurst Island is located in the Parry Island group of the Canadian Arctic Archipelago (Figure 3). The Bathurst Island complex covers about 18,000 km^2, most of which is under 300 m (1,000 ft) in elevation. The irregular coast features several long inlets, two of which, Bracebridge and Goodsir, almost bisect the island. The broad valley lying between these two inlets is known as Polar Bear Pass and this was the area in which this study was undertaken (Figure 4).

The hills to the north of this valley are long, regular, east-west folds of Ordovician to Devonian limestones and shales (Blake, 1964) and are generally under 180 m (600 ft) in height. To the northeast, the limestone hills rise to an elevation of 240 m (800 ft) within 8 km of the valley proper. Several streams and rivers flow south

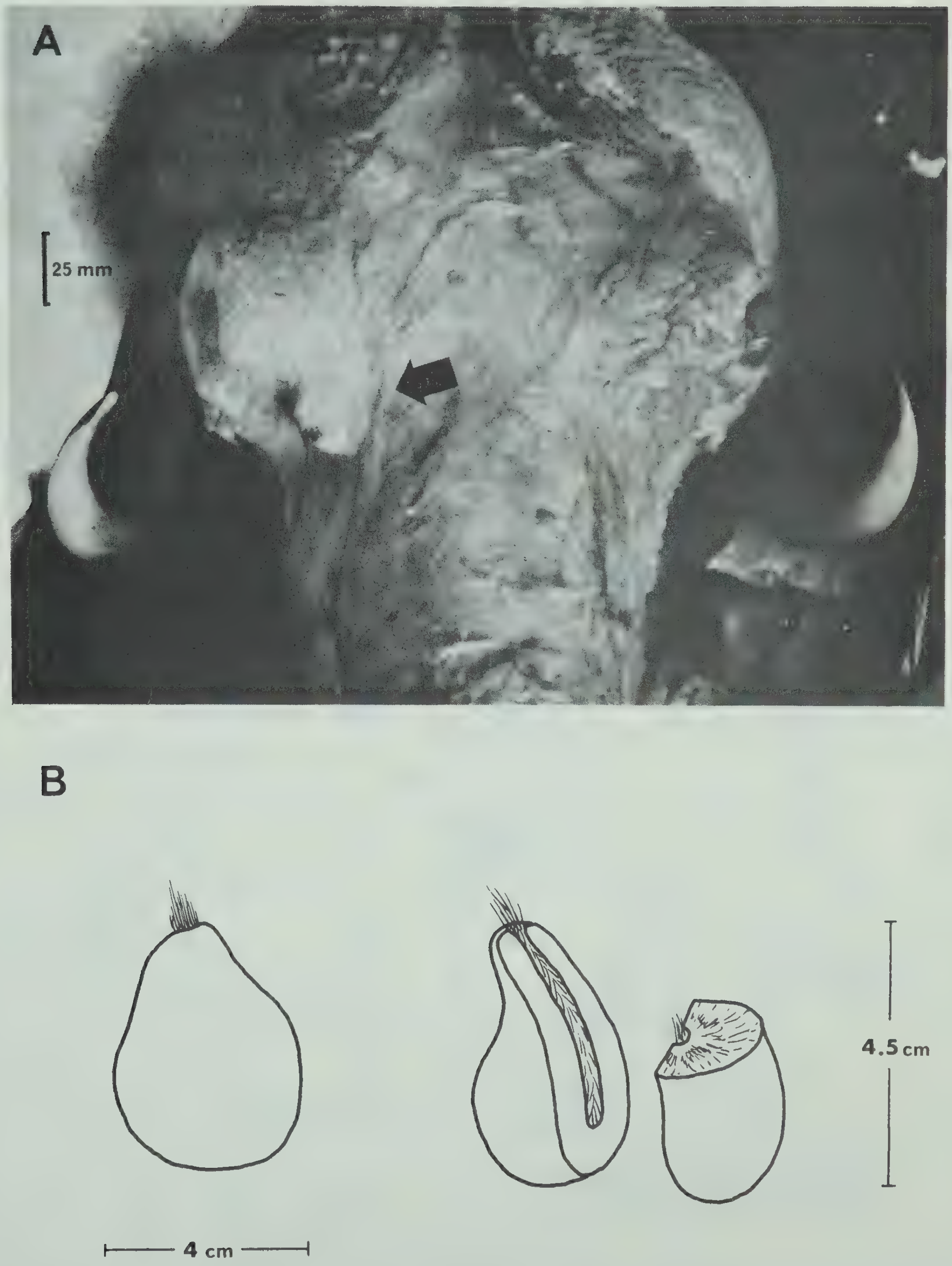

Figure 2 Location and structure of muskox preorbital glands. A - Head of adult female showing position of intact gland. B - Adult male preorbital gland.

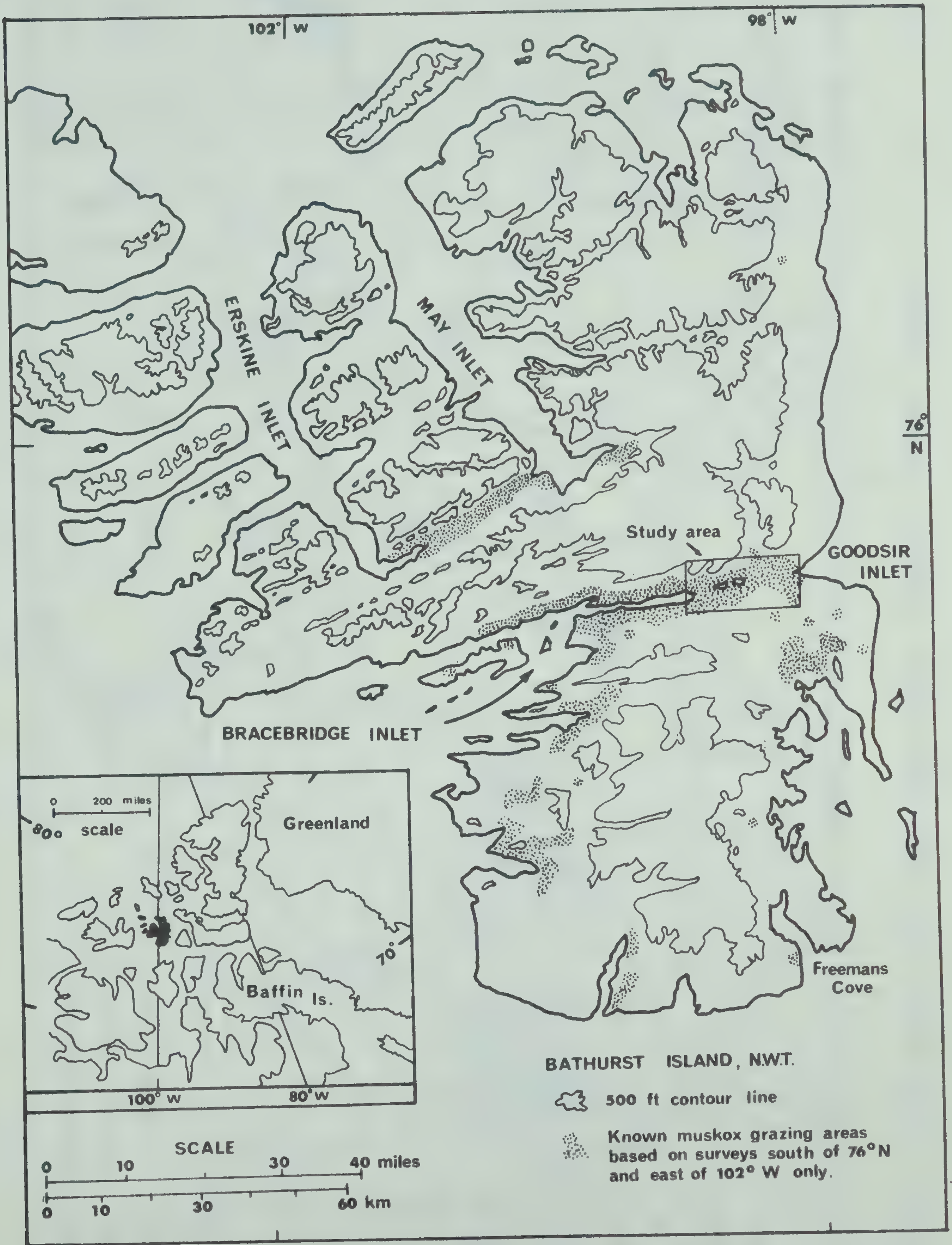

Figure 3 Bathurst Island, N.W.T., showing known muskox grazing areas on the southern portion of the island.

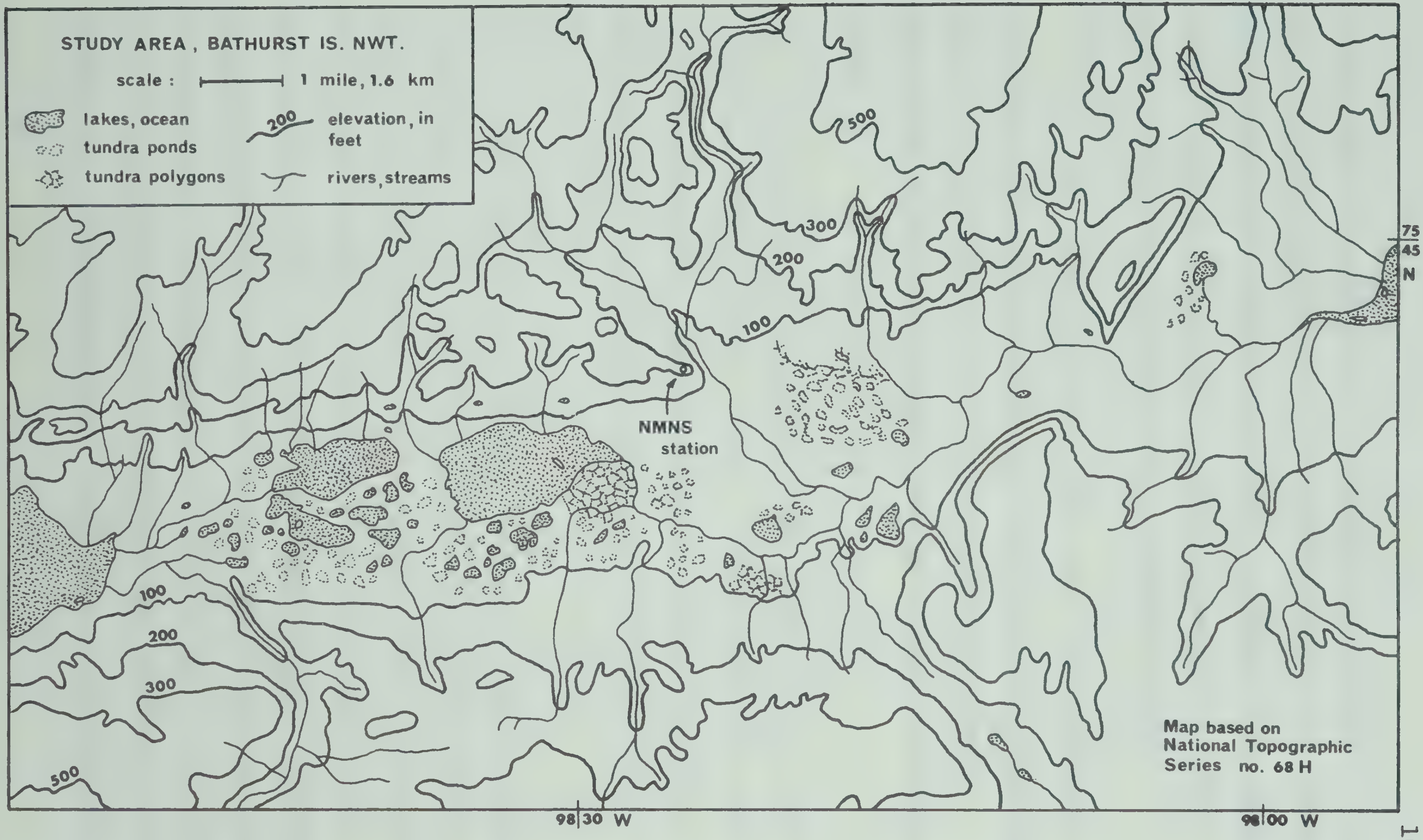

Figure 4 The study area, Polar Bear Pass, Bathurst Island, N.W.T.

through these rolling hills, then east into Goodsir or west into Bracebridge Inlet. The largest river is the Goodsir which flows south across the valley, divides into several braided channels, is joined by several smaller streams, then swings north and east and into Goodsir Inlet.

To the south the hills are lower, less obviously east-west oriented and rise much more gradually from the valley floor. The major river to the south is the Caledonian which flows north, then west into Bracebridge Inlet.

The valley of Polar Bear Pass is 40 km long and about 2 km wide. Approximately 75 km^2 of the valley is under 30 m (100 ft) elevation. Two large lakes, several smaller lakes, and many marshy ponds occupy much of the valley floor (Figure 4).

This marshy, wet tundra area is of great importance to muskoxen. Due to the permafrost below a shallow active layer, water does not drain off quickly and is available to many plant species. Around the ponds and lakes, several species of grasses and sedges (eg. *Carex stans*, *Eriophorum scheuchzeri*) form a lush growth seen only in a few other restricted areas on the island. In many parts of the study area, this wet meadow is modified by the presence of frost mounds, low and high centered polygons and the dendritic

patterned ground of the peat hillocks which develop along certain stream beds. The bases of these landforms are wet and covered with grasses and sedges, on the sides appear such flowering plants as the mountain sorrel (*Oxyria digyna*) and arctic poppy (*Papaver radicatum*), and on the drier tops appears several species of lichens.

At a slightly higher level, i.e., on the river terraces, raised beaches or strandlines, the vegetation is characterized by an almost continuous mat of lichens, interspersed with mosses, sedges, grasses, various species of saxifrage, mountain avens (*Dryas integrifolia*) and arctic willow (*Salix arctica*).

Higher up the hill-slopes the permafrost level is lower and drainage is good. The vegetation becomes sparser and the plants grow in more and more widely separated clusters or tussocks. On the tops of the hills and ridges only widely scattered plants of mountain avens, purple saxifrage (*Saxifraga oppositifolia*) and arctic poppy occur together with the omnipresent lichens.

Large areas at higher elevations (i.e., over 180 m) and smaller areas on most hill-tops are virtually devoid of vascular vegetation. These areas are, in fact, arctic deserts. Fellfields, limestone felsenmeer, rock circles, patterned ground and solifluction slopes all occur on the

surrounding hills (terminology follows Bird, 1967). Frost-thrust plates line certain ridge tops, a very few glacial erratics and several tors occur on others. Apart from these latter forms, the study area is generally flat or rolling with little relief and few obstructions to vision.

The major herbivorous species sharing the Polar Bear Pass area with the muskoxen are Peary caribou (*Rangifer tarandus pearyi*), arctic hare (*Lepus arcticus monstrabilis*) and varying lemming (*Dicrostonyx groenlandicus*). As the name suggests, polar bears (*Ursus maritimus*) travel through the valley relatively frequently in summer. Bears have, on occasion, eaten from muskox carcasses and arctic foxes (*Alopex lagopus innuitus*) regularly feed on such remains. Of the forty or so species of birds that reach the study area in summer, at least three -- Glaucous and Thayer's gulls (*Larus hyperboreus* and *L. thayeri*), and the long-tailed jaeger (*Stercorarius longicaudus*) -- also scavenge food from winter- and wolf-killed muskoxen. Snowbuntings (*Plectrophenax nivalis*) feed on insects around carcasses and they and Lapland longspurs (*Calcarius lapponicus*) build nests with muskox wool. Arctic wolves (*Canis lupus arctos*), the only present day predators of the muskoxen of this area, travel along the valley in small packs or in pairs at near regular intervals.

The National Museum of Natural Sciences High Arctic

Research Station is located mid-way between Bracebridge and Goodsir Inlets on the north side of the valley. The station sits on a 60 m (200 ft) ridge overlooking both the main valley and the upper Goodsir River valley.

The climate of the Arctic Islands, including Bathurst, is, for most of the year, a continental type climate, somewhat modified by the relatively warm water beneath the winter ice (Thompson, 1967).

The following description of the climate on a year-round basis is based on our own observations (See Table 1) and Thompson's (1967) description of the arctic climate in which he divides the year into four periods, only roughly corresponding to the familiar four seasons of southern Canada.

May-June ("Spring")

In May, after the advent of 24 hours of sunlight, temperatures climb steadily to above the freezing point. Increased cloudiness and snowfall are normal, though in some years, clear skies in May are frequent. Temperatures in June are generally above freezing and the snow melts quickly. Low clouds and fog are common as southern air passes northward over the extensive ice surfaces.

Table 1. Summary of weather data recorded at the NMNS Research Station, Bathurst Island from April 1970 to April 1971

Month	Temperature Extremes (F) Max.	Min.	Mean Temp. (F)	Mean Wind speed (mph)	Total ppt. (in)	No. of days visibility less than 2 miles*
Apr. 70**	10	-32	-13.2	8	-	0
May 70	48	-17	12.4	10	0.01	3
June 70	52	14	31.9	13	0.06	6
July 70	61	32	42.5	11	0.23	3
Aug. 70	54	19	37.0	8	0.75	2
Sept. 70	33	1	23.1	8	0.16	8
Oct. 70	30	-19	1.1	9	0.26	13
Nov. 70	26	-45	-16.8	12	0.10	16
Dec. 70	-8	-47	-29.2	10	0.09	19
Jan. 71	0	-52	-33.3	16	tr.	11
Feb. 71	-10	-46	-31.5	10	0.05	9
Mar. 71	-2	-40	-21.8	9	0.04	5
Apr. 71	25	-42	-9.3	11	0.05	10

* for at least ½ day

** 14 days only

July-August ("Summer")

July and August are the wettest months of the year with the combined monthly totals of precipitation reaching at least 1 inch (2.5 cm). Temperatures average 40 F (4.4 C) and again, fog and low clouds are common. In early July, the rivers break up and water floods out over many low-lying areas. By August of most years, only a few snowbanks remain in sheltered areas and by the end of the month, the sun is again dipping below the horizon.

September-November ("Fall, early winter")

By early September, daily temperatures are below 32 F (0 C) and by mid-October, temperatures below 0 F (-17.8 C) are common. Storms are most frequent in this period with much of the year's snowfall coming at this time. Cold, clear weather follows the freeze-up of open water in November. The last sunrise-sunset of the year occurs in the first week of November.

December-April ("Winter")

Despite the absence of direct sunlight from early November to early February, the high arctic is not a region of "24 hours of darkness." The mid-day twilight, even on 21 December, provides enough light at this latitude for the usual outdoor activities. On clear days, the starlight re-

flected from the snow-covered landscape is sufficient for travelling on foot. For about one week on either side of the full moon, landforms up to 5 km distant can be seen easily. The daily temperatures for December, January and February averaged about -30 F (-34.4 C). Although these months are usually clear as well as cold, December 1970 was stormy and the combination of low light and high frequencies of snow and blowing snow resulted in poor to zero visibility for almost two-thirds of the month. The minimum temperature reached at Bathurst during this study was -52 F (-46.7 C), recorded on 27 January, 1971, following five days of temperatures below -45 F (-42.8 C). Ice fog is common during very cold weather because of open leads in the pack ice off the island coasts.

Although direct sunlight returns to this area in early February, its effect on daily temperatures is not felt until April. Following five months of below-zero temperatures (F) in the winter of 1970-71, the temperature rose to 13 F (-10.6 C) on 17 April. By the end of April, the sun is again above the horizon for the full 24 hour day.

Meteorological data recorded during 1970-71 have been compared with those recorded at Resolute Bay on Cornwallis Island (140 km southeast) during the same time period (Thompson, 1971). She found that, in general, the two sta-

tions experience similar climatic conditions with Bathurst Island having slightly colder winters and warmer summers than Resolute.

Variations in the timing of the spring melt and in the break-up of river and lake ice were noticed during the four years of the study. Although no quantitative studies of the vegetation in the study area have been conducted, there was a noticeable increase in size and number of flower heads of several species, especially Eriophorum, from 1968 to 1970. A trend towards longer "summers" was evident between 1968 and 1970. Meteorological records for Resolute Bay indicate this same trend and also show a succession of relatively short summers (i.e., number of calendar days with ground free of snow) in the 4 years preceding the initiation of this study (Figure 5).

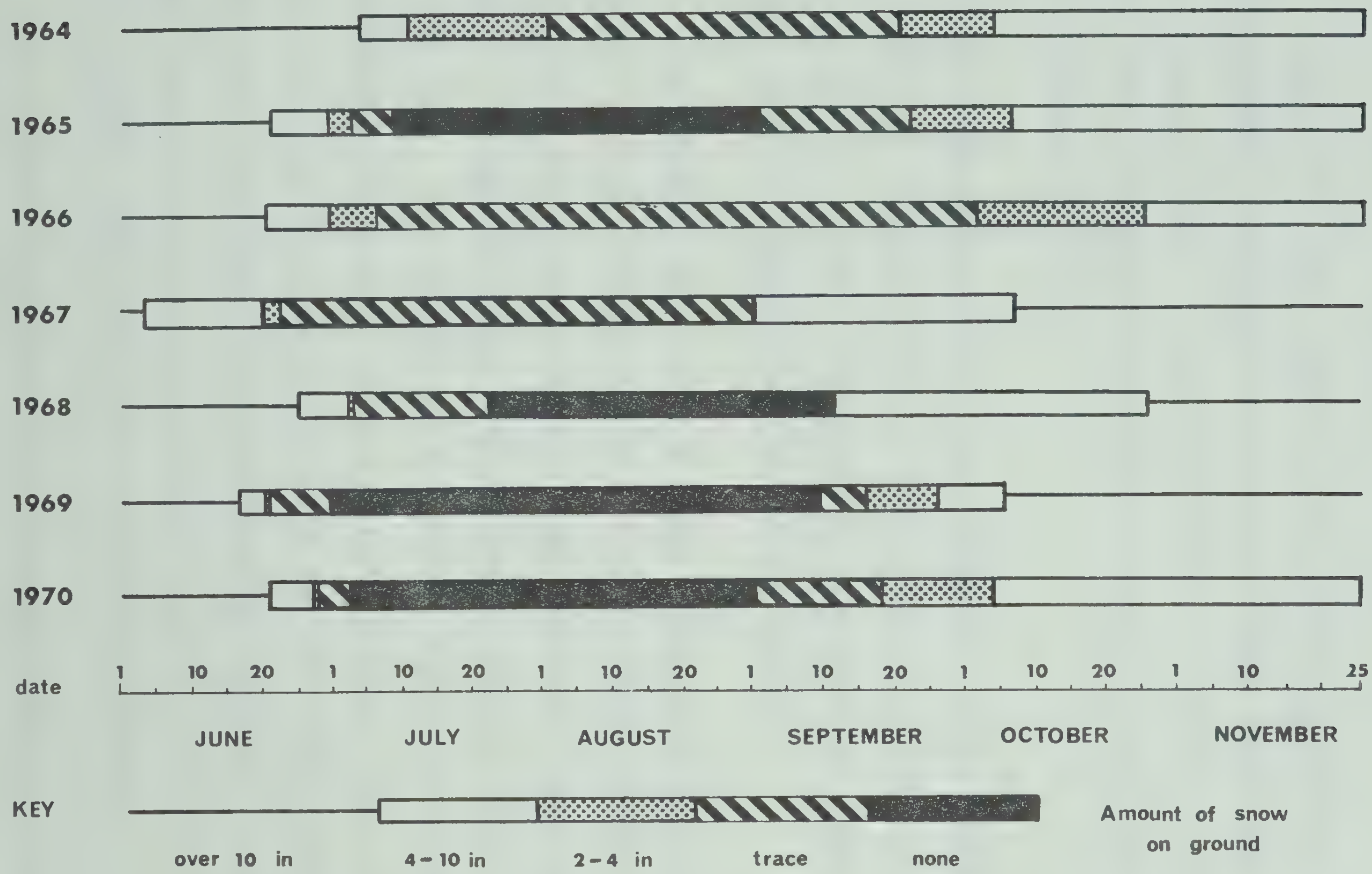

Figure 5 Days with trace of snow and no snow on the ground at Resolute Bay, N.W.T. in the period June to September, 1964 to 1970.

METHODS

The total time spent in the field during this study was 22 months, covering the following time periods: 20 May to 14 August 1968, 29 April to 27 August 1969, 12 April to 5 June 1970, 14 August 1970 to 11 June 1971 and 28 August to 27 October 1971.

Living quarters for the duration of the study were two 16x16 ft. Parcoll huts at the N.M.N.S. Research Station. For the winter study, the station consisted of these huts and one 16x8 ft. fiberglass storage "igloo."

Throughout the study I made daily counts of the muskoxen in the study area from the vicinity of the camp using 15x60 and 25x60 Bushnell "spacemaster" spotting scopes. The approximate area surveyed during these counts was 140 km^2. The extent of the study area was in part determined by the area of the valley visible from the camp ridge. During June and July 1970 and 1971 the muskox counts were continued in my absence by Philip S. Taylor. These observations are incomplete because of his own research commitments which prevented daily counts.

In winter, we travelled from the camp to herds under

observation by snowmobile or cross-country skis, the latter being much more reliable and efficient during the three coldest months. In summer we followed herds on foot. On a few days muskoxen could be observed directly from camp; at other times, I had to walk distances of up to 16 km before beginning observations.

The area visible from camp decreased in the late fall as the amount of daily light decreased. Between 26 November 1970 and 15 January 1971, the radius of visibility, using the spotting scope, was always less than 9 km and often close to zero. Mobility of the observers also decreased in mid-winter due to minor medical problems and constant mechanical difficulties.

Several aerial surveys were conducted during the study in order to determine the distribution of muskoxen on the island (Figure 3). Results of these surveys have been reported elsewhere (Gray 1970, 1971).

Observation Techniques

During summer we were able to maintain observation periods for up to 12 hours with little difficulty. In the early phases of the study I recorded behaviour and activity at all times of the 24 hour day. Later observations were generally restricted to between 0800 and 0100 C.D.T.

Whenever possible, I made observations from downwind and from at least partial concealment. Because of the nature of the landscape, the latter was not often possible. When there was no concealing cover, a distance of about 270 m was maintained from the herd. Observations were made at distances ranging from 9 m (infrequently) to 9.5 km. Except during the peak of the shedding season, sexes could be distinguished effectively at a distance of 1.5 km (under optimum weather conditions). Blinds were not used because of the virtually constant movements of the herds.

While observing muskoxen in winter, we made full use of the snow and natural landforms as shelter. This, in combination with the usual techniques of keeping extremities moving and alternating note taking with intervals of intense activity, allowed us to maintain observations over several hours, even during extreme cold. When observing from an exposed position, we wore white camouflage suits over parka and pants.

I recorded all observations in notebooks except when the action of the animals required a faster recording method. A portable Sony cassette tape-recorder was used in these circumstances, and to record activities of special significance in more detail.

I used a Pentax Spotmatic 35 mm camera with a 200 mm

telephoto lens plus an adaptor to fit the Bushnell Spotting Scope and a Bolex 16 mm movie camera with a 150 mm telephoto lens to record muskox behaviour patterns on film. Drawings of muskox behaviour patterns were based on photographs and field sketches.

Still and cine photography of the muskoxen became very difficult during the period of sub-zero temperatures and low light intensities. Although the Pentax was winterized, to ensure operation at low temperatures it had to be kept under the parka almost constantly, thus preventing the taking of useful photo sequences. Over 4000 feet of 16 mm film was used but very little of this was exposed during the four coldest months because of the slowing down of the Bolex drive mechanism. Use of the tape recorder was also restricted by the effect of low temperatures and the frequency of malfunctioning tapes.

The usual observation technique was to watch a single herd continuously throughout their feeding periods of the day. During the 1970 rutting season we collected data from as many as four or five different herds daily by recording only during the first and last parts of the feeding period of each herd.

During a typical observation period, I recorded the movement and activity of the herd, individual behaviour and all interactions between individuals. When I collected data

on activity patterns, I recorded the position of each animal in the herd and times of lying down and rising. For all interactions, I recorded, whenever possible, the duration of the act, the age and sex or identification of the individuals involved and behaviour patterns seen before and after the interaction.

One observer could usually keep track of all obvious interactions in herds of up to 10 animals. For larger herds or when herds were spread out, I recorded activity in one half of the herd only. During poor weather in winter, we usually worked together, one of us observing and the other recording.

Through daily observations, I was able to record the movement of individual herds through the study area and the relationships between these herds. Joining and splitting interactions were recorded in a flow diagram (Appendix I). Each herd which remained in the study area for over 3 days was given a label indicating the year, the position in the flow diagram and the size of the herd, eg. 68-A-7. Herds that were observed over a long period of time, and the dates of observation, the sex ratio and known individuals in the herds, are listed in Appendix II.

Eight mineral salt and cobalt salt blocks were set out in known muskox feeding areas. I had hoped that wild muskoxen would find them as attractive as captive muskoxen

do (Oeming 1965) and that interactions around the blocks might help in determining social structure. However, the few muskoxen that did pass close to the blocks while feeding, paid no attention to them.

Observations of temperature, wind, precipitation, cloud cover and visibility were taken twice daily (for summary, see Table 1). The complete weather records are on file at the National Museum of Natural Sciences, Ottawa and the Atmospheric Service of the Department of the Environment.

Determination of Age and Sex

Determination of the sex of adult muskoxen was based on horn structure, body size, hair length and urination posture. Age was more difficult to determine because of the absence of some age classes in the population (few subadult bulls were present and calves were absent, as were yearlings and two-year-olds). Subadult bulls between the ages of three and six were classified according to Allen (1913) and Tener (1965). Bulls older than about 6 years were classified as adults. Since no cows were observed that appeared to be 2 years old or younger, all cows were classified as adults for the purposes of this study.

Marking Techniques

Although individuals in a small herd could be recog-

nized by their body size and the size and shape of their horns, it was desirable to mark individuals to increase the amount of information obtainable on the movements of herds and on individual behaviour and activity. Several different techniques were tried, each requiring the approach of several persons to a herd in the tightly grouped defence formation.

On 21 July 1969 we approached to within 13 m of a herd of six (1 bull, 5 cows) during a heavy rain and strong wind. Numbered streamers of bright red plastic wired to three-pronged fish hooks and loosely wrapped around small stones were tossed downwind into the herd. As the herd bolted, two sets of streamers hooked into the wool of the bull, one of which still remained attached when the herd was next seen, 14 days later. A cow in a group of 10 cows was marked in a similar fashion on 6 August. Again, after the initial throw, the herd ran off into the hills and out of sight. We marked a second cow on 27 August 1969. On 13 May 1970, we marked five animals in a herd of eight muskoxen with streamers and enamel paint fired at the horns from a Nelspot paint-pellet pistol (The Nelson Paint Company, Iron Mountain, Michigan, U.S.A.). These techniques were not used often because of the risk of driving off the few herds present in the study area.

On 25 and 26 July 1968, we made several unsuccessful attempts to drug and tag a solitary adult bull from the

ground, using a powder-charge dart gun ("Cap-chur" gun, Palmer Chemical Co., Douglasville, Georgia, U.S.A.) and darts containing succinylcholine chloride ("Anectine," Burroughs Wellcome and Co., Montreal).

In mid-May 1970 four bulls and two cows were immobilized and tagged using the Cap-chur gun technique and a Bell G47 helicopter (Jonkel, 1971). Six additional bulls were ear-tagged with nylon "Leadertags" and plastic "Permatags" (Ketchum Manufacturing Sales Ltd., Ottawa) in May 1971. Plastic streamers were attached to the horns with metal hose clamps and radio transmitter collars were fitted around the neck. The drugging and tagging techniques will be reported elsewhere (Jonkel and Gray, n.d.).

Unfortunately, the necessary funds and logistic support for the tagging procedure were not available early in the study. Also, the technique of using a helicopter to isolate one animal from a herd caused an undesirable amount of disturbance to the herds and so we marked only a very few muskoxen in the study area proper (Figure 6). Consequently, there were few opportunities to record the behaviour and activity of tagged animals within herds under observation.

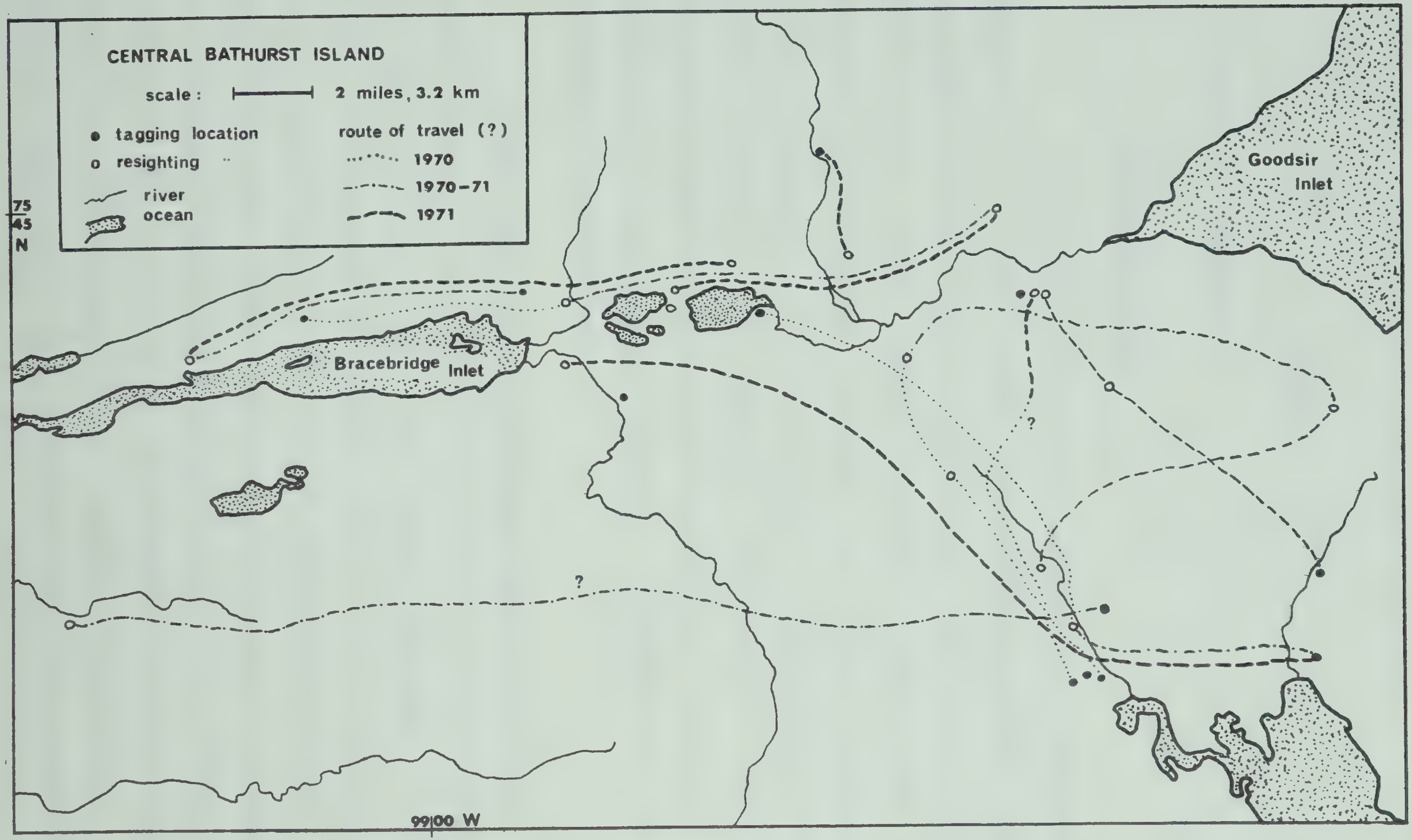

Figure 6 Locations of tagging and resightings of tagged muskoxen in central Bathurst Island and probable routes of travel between the locations.

RESULTS

I. THE STUDY POPULATION

A. Recent History

Since 1930, there have been several published estimates of the total muskox population on Bathurst Island. Anderson (in Hoare, 1930) estimated the population to be 1500 muskoxen. Tener (1958) estimated the total number of muskoxen on the island to be about 100. After "intensive" aerial coverage of the island, McNair (in MacPherson, 1961) made an estimate of 300 muskoxen. As a result of the Queen Elizabeth Islands Game Survey in 1961, Tener (1963) re-estimated the population, arriving at a figure of 1,161 muskoxen on the island.

In the past, the Bracebridge-Goodsir valley was known locally as the "zoo" because of the numbers of caribou and muskox occupying the valley during the summer. In June, 1957, Thorsteinsson (MacPherson, 1961) saw 149 muskoxen during a single flight in the Bracebridge-Goodsir valley. In June 1961, Tener (1965) saw 4 herds containing 69 animals on the south shore of Bracebridge Inlet. On a flight from north of Goodsir Inlet south to Freeman's Cove in August, 1964, L. V. Hills (pers. comm.) counted 150 muskoxen. Most of these animals were observed within the Bracebridge

and Goodsir Inlets.

During this study, the number of muskoxen in the Bracebridge-Goodsir valley (i.e. the study area) fluctuated from 0 to 121 (Figure 7). The mean herd size ranged from 4 to 29 (Figure 8) and the greatest number of herds in the study area ranged from 1 to 16 (Figure 9).

In demonstrating the change in total number of musk-oxen, mean herd size and number of herds in the study area (Figures 7-9), and in summarizing these data for each month of the study (Table 2), I have used the highest recorded number of each week of the study rather than the mean for each week because of the many days when accurate counts were impossible due to weather conditions.

An important feature of this population was the steady increase in numbers in the study area during late summer and fall (Figure 7). At that time, herds moved into the area from the east, west, north-west and south. The increase in numbers reached its peak at 115 muskoxen on 25 August 1969, 121 muskoxen on 3 October 1970, and 110 on 10 October 1971.

In 1970, the size of the population decreased rapidly after October as herds moved out of the area. No muskoxen were seen in December 1970 or January 1971. The only other times when muskoxen could not be found in the study area were early July 1968 and the last half of April 1971. The numbers

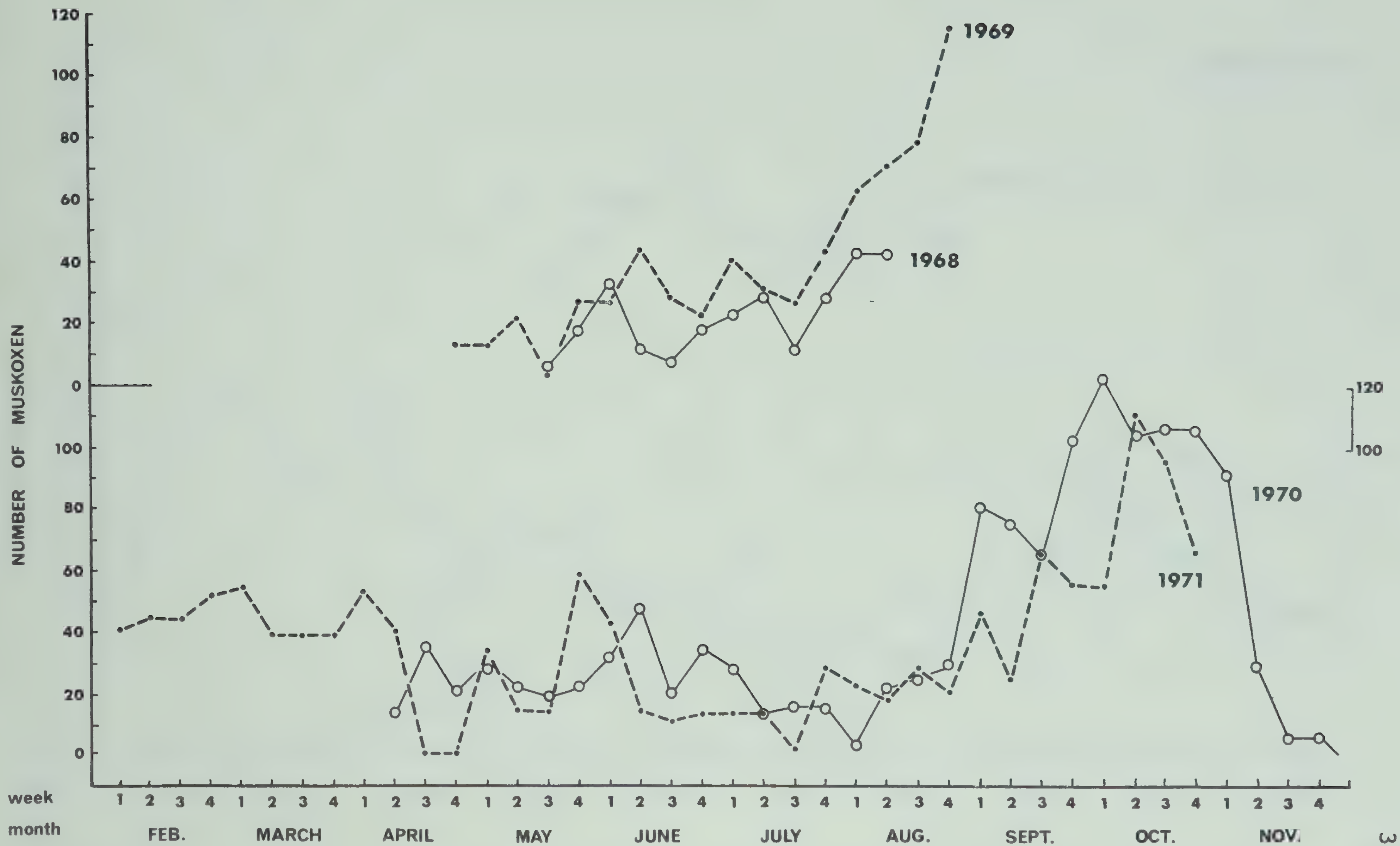

Figure 7 Highest number of muskoxen in the study area for each week of the study, 1968 to 1971.

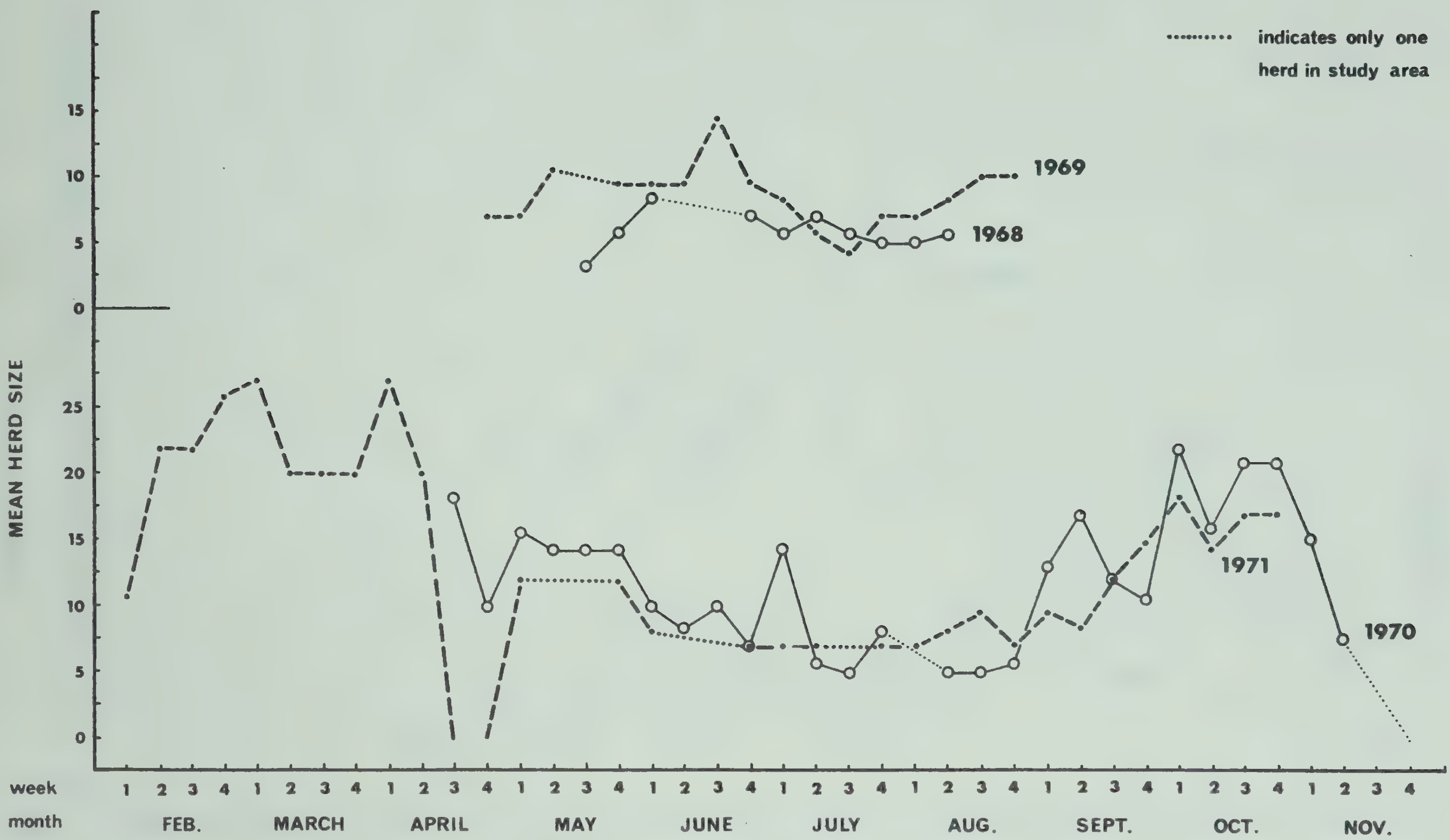

Figure 8 Highest daily mean herd size in the study area for each week of the study, 1968 to 1971.

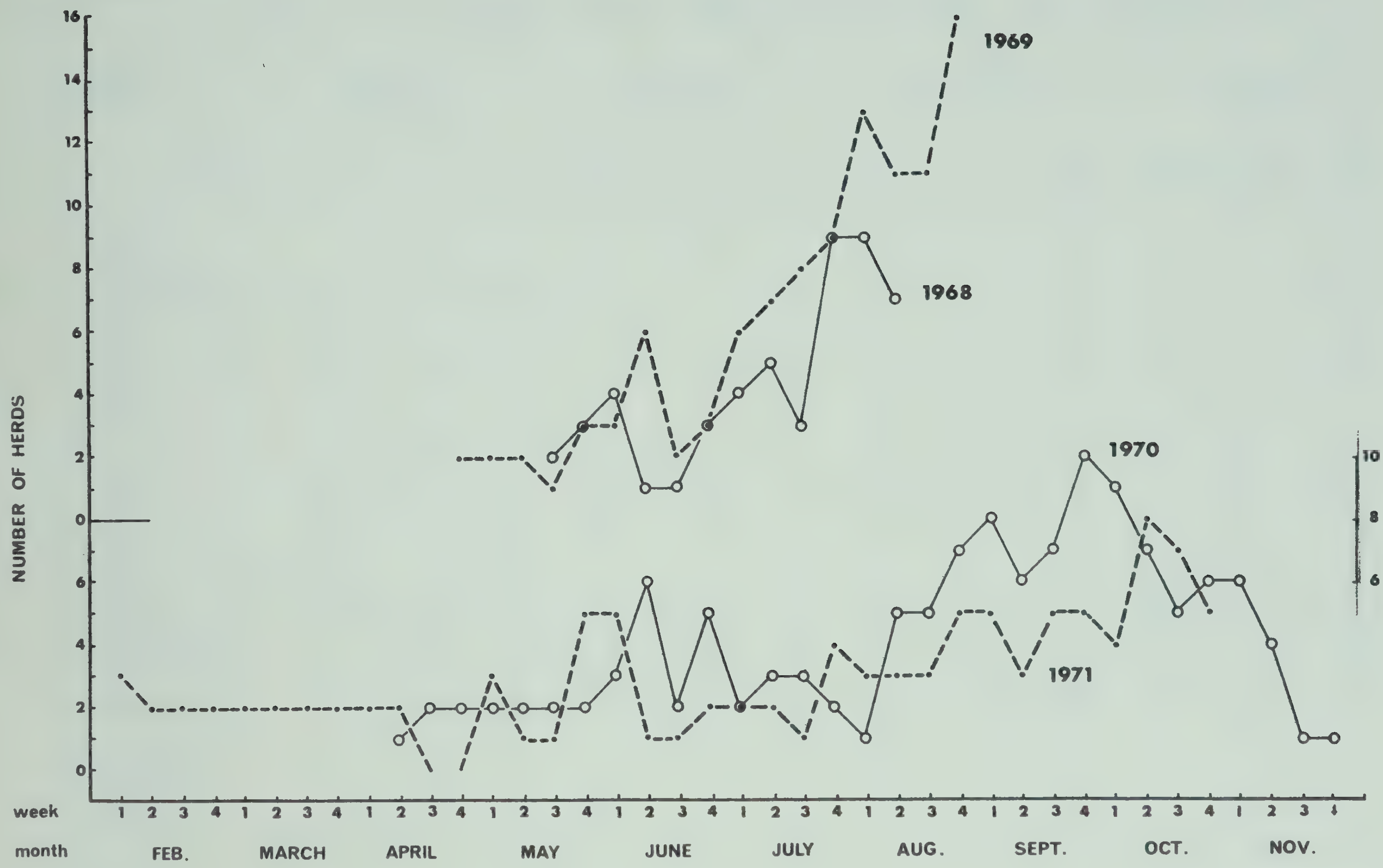

Figure 9 Highest number of herds in the study area for each week of the study, 1968 to 1971.

Table 2. A summary of the seasonal changes in study population numbers and herd sizes in the Bathurst Island study area from May 1968 to October 1971.

Month	Highest Daily Total				Highest No. of Herds				Mean Herd Size				Largest Herd			
Year	68	69	70	71	68	69	70	71	68	69	70	71	68	69	70	71
January	-	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0
February	-	-	-	51	-	-	-	3	-	-	-	22	-	-	-	41
March	-	-	-	53	-	-	-	2	-	-	-	21	-	-	-	33
April	-	-	35	53	-	-	2	2	-	-	13	29	-	-	21	40
May	17	48	30	59	3	5	2	5	5	10	8	10	11	16	16	18
June	32	58	48	42	4	6	6	5	6	9	8	8	11	25	16	18
July	28	43	28	28	9	9	3	4	4	6	7	7	8	18	21	8
August	42	115	28	27	9	16	7	5	5	7	4	6	12	20	10	12
September	-	-	101	64	-	-	10	5	-	-	11	9	-	-	35	27
October	-	-	121	110	-	-	9	8	-	-	18	15	-	-	53	32
November	-	-	90	-	-	-	6	-	-	-	12	-	-	-	31	-
December	-	-	0	-	-	-	0	-	-	-	0	-	-	-	0	-

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seen in February and March 1971 were higher than the average summer population but not as high as the fall population.

In the spring and summer of 1968, 13 muskox carcasses were found in the study area. Of these animals, three adult females and three adult males had died the previous winter, one calf (estimated to be 6 months old) had died the previous fall or early winter and one adult female and two subadults (about 2 to 3 years old) had probably died within the previous 2 or 3 years. All but one of the recent carcasses were untouched by scavengers, indicating death due to factors other than predation. Another adult bull died on 31 May 1968. Femur marrows of that bull, one of the adult cows and a subadult bull killed by a wolf on 28 May, 1968, were found to be red and jelly-like, suggesting nutritional stress at the time of death (Cheatum 1949). Marrow from the femurs of an adult bull accidentally killed during the tagging procedure in May 1971 and a pregnant cow killed by wolves in March 1971 were found to be white, firm and waxy (Hubert, pers. comm.) indicating good condition. No carcasses other than the two resulting from wolf predation were found in the study area after 1968.

B. Distribution of Muskoxen in the Study Area

Between February and April muskoxen fed along the north side of the main valley at the foot of the south facing

slopes (Appendix III, part 1). Some herds were found between the ridges and in several of the smaller gullies north of the valley and at the east end of Bracebridge Inlet. In May, the herds grazed in valleys offering relatively shallow snow and some shelter from the wind. During June, the muskoxen extended their feeding areas to the east, feeding at the foot of the slopes where wind-blown material on the snow surface caused an early melt. A few herds were observed on the south side of the valley near Bracebridge Inlet (Appendix III, part 2). As the snow began to melt, the muskoxen moved more and more to the exposed areas, feeding on such plants as: *Carex stans*, *Saxifraga oppositifolia* and *Salix arctica*. During July, as more herds moved into the valley, much of the ground in mid-valley was utilized (Appendix III, part 3). By mid-August, the muskoxen were feeding in and around the wet, marshy areas over the whole valley using, among other plants, *Carex stans*, *Arctagrostis latifolia* and *Eriophorum scheuchzeri*. In late August, most of the herds were on the south side of the valley, both down in the marsh and up on the gentle, north-facing slopes. In September and October, herds were feeding in mid-valley, mainly around the edges of the many ponds (Appendix III, part 4).

In October and November, 1970, herds moved out of the study area to the west. Most herds moved along in their usual slow, walking manner, but in other cases (e.g., a herd of 31

on 1 November), the whole herd moved west, alternating galloping and walking, with little pause for feeding, until they disappeared from view. By November 12, only one herd (70-E-14) was visible from camp. No muskoxen were seen during trips to various parts of the study area from 27 November 1970 until 4 February, 1971.

Although some herds remained in the study area for less than 24 hours, others spent over a month within the study area boundaries. For example, herd 69-A-4 remained within an area of approximately 20 km^2 from 29 April to 30 July, 1969 and two other herds (70-E and 70-F), in the period from 6 September to 5 November, 1970, remained within areas of 9 and 11 km^2 respectively (Appendix III, part 5).

Resightings of tagged and marked muskoxen showed that individuals (in herds) do move between the study area and other areas of muskox concentrations up to 37 km distant (Figure 6). Four of the six tagged in 1970 and three of the six bulls tagged in 1971 have been resighted in the study area.

C. Discussion - The Study Population

The estimates of the size of muskox population of Bathurst Island cannot be compared with any confidence because the surveys undertaken were not standardized. Surveys conducted during this study (Gray 1970, 1971) have demon-

strated the great differences in total counts that can result when surveys over one area are made during different seasons. Fluctuations in numbers obtained in the daily counts from the ground (Figure 7) indicate that short term surveys may be unreliable for estimating the size of a local muskox population.

Seasonal changes in distribution of the muskoxen in the study area followed a similar pattern in each of the four years of the study. Rather restricted distribution during the late winter, spring and early summer accompanied low population numbers. As the local population increases during the summer, more and more of the valley area is used by the incoming herds. This wide distribution accompanying the increase in number of herds and in the mean herd size may be important in relation to the number of interactions between herds seen at this time (Appendix I). The influx of herds into the lowlands of the study area in late summer coincides with the end of the reported rutting season and may be influenced by early snowfalls at higher elevations which may cover the ground "permanently" as early as the end of August.

The significance and possible causes of the mortality evident in the spring of 1968 will be discussed in following sections.

II. SOCIAL ORGANIZATION

In this thesis, I use the term "herd" to describe any group of two or more animals in which the individuals are usually separated by a distance of less than about 100 m and have synchronized activity patterns, i.e., they move, feed and rest together.

A. Herd Structure and Composition

1. Herd Size

The monthly mean herd size in the study area as determined from the daily counts, changed from a low of 4-7 in July-August to highs of 15-18 in October, 21-22 in February-March and 13-29 in April (Table 2). In the fall of 1969, 1970 and 1971, the mean herd size generally increased along with the total number and the number of herds (Figures 7-9). The most frequently observed herd sizes for each month in the four years of the study were similar (Appendix IV). In summer, the most frequently observed herd sizes were in the three to six range while in winter, the most frequently observed herd sizes were much more variable, ranging from five to over 15.

2. Solitary Bulls

Three solitary bulls were seen in 1968 (20 May, 28 May and 24 July) and 1969 (24 June, 5 July, 5 August). From

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April 1970 to October 1971 seven solitary bulls were observed in the study area, three of them marked bulls temporarily separated from herds after the tagging procedure. One is thought to have dropped out of a herd stampeded after a wolf attack and one was a dominant bull who simply walked away from his herd (70-E-15) and was not followed (September 5, 1970). Only two other solitary individuals were seen (9 June 1970, and 28-30 August 1971). Two other solitary bulls were seen on surveys outside the study area - an adult on 19 August and a 3 or 4 year old subadult on 23 May 1970. No solitary cows were seen during the entire study.

3. Age Composition

The muskox population of the study area consisted mainly of adult animals. No yearlings were observed during the study and no calves were seen until 20 September 1971, when one calf was seen in a herd of 27 at the east end of Bracebridge Inlet. This was the only calf seen in my study area (excluding the foetus recovered from a wolf-killed cow in March 1971 and the carcass of a calf estimated to be six months old, found in June, 1968). Unfortunately, after only 1½ hours of observation, this herd stampeded away with the calf after an unsuccessful wolf attack. Five subadult bulls were seen in the study area in the summer of 1968 and 8 in 1969. Eight subadult bulls were observed from April 1970 to September 1971 (Appendix V).

Outside the study area the first calves were seen on 1 and 2 May 1971 during a helicopter survey of southern Bathurst Island. Five calves were seen each in a different herd. The total number of muskoxen seen on those two days was 196. Many of these same herds were surveyed on 13 April from a Twin Otter aircraft but no calves were seen. Five additional calves were seen with a herd of 8 adults at the south-east end of Bathurst Island on 17 May 1971 and 6 calves of unknown sex were seen in a herd of 29 (13 cows, 10 bulls) at Freeman's Cove (Figure 3) on 4 October 1971.

During the helicopter surveys outside the study area in May 1970 and 1971, only 8 subadult bulls were seen (one, a 5 or 6 year old, was tagged as bull #71-2).

4. Sex Ratio

Because of the disruptive effect of close approach by humans, it was not feasible to determine the sex ratio of all herds seen in the study area. Approaching large herds closely enough to determine sex ratios often led to stampede. In late summer and fall we could not approach a herd close enough to determine the sex ratio without alarming the other herds in the area.

Because of mixing (see Herd Stability), animals included in the ratio for one month may also have been included in the ratio for the following month, but as part of a dif-

ferent herd.

In 1968 and 1969 the adult sex ratio approximated equality (Table 3). If single sex herds were included the sex ratio was slightly unbalanced in favour of bulls. The 1970-71 herd sex ratios, on a monthly basis and excluding solitary bulls and single sex herds, also approached equality (Table 4).

5. Single Sex Herds

Three herds of bulls were seen in 1968 (n= 2,4,4). In 1969, 15 herds containing only bulls (mean herd size 3.5) and 4 herds containing only cows (mean size 5.5) were observed. In 1970 (May-December) nine bull herds (mean size 4.2) and one herd of four cows were seen (Appendix VI). Between May and October 1971, only two bull herds were observed in the study area and another seven on aerial surveys (mean for all 9 = 4.4).

6. Discussion - Herd Structure and Composition

The seasonal change in herd size from large winter herds to smaller summer herds corresponds to the situation reported by Tener (1965) for other Canadian muskox populations and by Spencer and Lensink (1970) for the muskoxen of Nunivak Island, Alaska. The number and size of the single sex herds observed in this study also matched their findings.

Table 3. Adult sex ratio in muskox herds in the study area in 1968 and 1969.*

Month	No. of Herds	No. of Bulls	No. of Cows	Total	% Bulls for month	No. of Bulls per 100 cows
1968						
May	1	6	5	11	54.5	
June	2	9	3	12	75.0	
July	6	18	8	26	69.2	
August	1	3	4	7	42.9	
Total	10	36	20	56	64.3	180.0
1969						
April	2	11	2	13	84.6	
June	8	30	47	77	39.0	
July	15	43	43	86	50.0	
August	12	35	46	81	43.2	
Total	37	119	138	257	46.3	68.2

* excluding single sex herds and solitary bulls.

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Table 4. Adult sex ratios in muskox herds in the study area in 1970 and 1971.*

Month	No. of Herds	No. of Bulls	No. of Cows	Total	% Bulls for month	No. of Bulls per 100 cows
1970						
April	1	7	7	14	50.0	
May	4	18	17	35	51.4	
June	1	2	2	4	50.0	
August	1	4	3	7	57.1	
Sept.	6	26	34	60	43.3	
Total	13	57	63	120	47.5	90.4
1971						
March	1	2	7	9	22.2	
May	6	31	24	55	56.4	
June	2	11	2	13	84.6	
Sept.	5	37	50	87	42.5	
Oct.	4	34	21	55	61.8	
Total	18	115	104	219	52.5	110.6

* excluding single sex herds and solitary bulls.

The two major differences between the composition of herds in my study area and in herds described by the above authors are in the observed age structure and in the sex ratio of mixed herds.

The complete absence of calves, yearlings and two-year olds during 1968, 1969 and 1970 is a marked change from conditions reported for earlier years. Tener (1963) reported that in the Bracebridge Inlet area in 1961, calves accounted for 27.5% and yearlings 18.8% of the observed animals (n=69). Hills (pers. comm.), in a flight over the study area in August 1964, distinguished 55 adults and 27 young. Because of clustering and the speed of the aircraft, he was not able to distinguish between calves and yearlings.

Several possible factors which could cause the observed decrease in the percentage of young muskoxen in the herds include failure of cows to come into full oestrus condition or bulls into rutting condition, loss or resorption of the foetus, winter mortality or heavy predation of calves. Certain of these factors may also be involved in the observed sex ratios in the herds studied.

In this study, even during the rutting season, the sex ratio in herds generally remained equal. In studies conducted elsewhere, the sex ratio in mixed herds was reported to be unbalanced in favour of cows, with rarely more than one

mature bull per herd (Tener 1965, for Ellesmere Island and the Thelon Game Sanctuary; Spencer and Lensink 1970, for Nunivak Island; and Hubert pers. comm., for Devon Island). These same investigators found numerous solitary bulls in summer and, in general, a one-to-one sex ratio when solitary bulls were included in the ratio. On Bathurst, bulls which would be expected to become solitary during the rut (on the basis of these other data), remained with the herds. The concensus of previous observers of muskoxen (Hone, 1934) is that bulls are expelled from herds after losing battles over the possession of cows during the rut. Therefore, before considering this situation any further, it is necessary to investigate the relevant aspects of herd dynamics and agonistic and reproductive behaviour.

B. Dynamics of the Herd

1. Activity Cycle

The activity pattern for muskoxen observed in this study consisted of alternating periods of feeding and resting-rumination each lasting for approximately 150 min (Tables 5-8).

Although the length of the periods for a herd on a particular day could be quite variable (Table 5), over a longer period of time the activity cycle for a single herd was relatively uniform (Table 6). A "typical" daily activity cycle consisted of a series of feeding and resting-rumination

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Table 5. The activity cycle of a herd of 10 muskoxen on September 15, 1970.

Time (CDT)	Herd Activity	Time Period (min)
0914	1st muskox down	
		40
0954	all 10 down	
	all resting/ruminating	110
1144	1st muskox up	
		32
1216	all 10 up	
	all feeding	208
1544	1st muskox down	
		91
1715	all 10 down	
	all resting/ruminating	90
1845	1st muskox up	
		37
1922	all 10 up	
	Total	10 hours, 8 minutes

Table 6. Activity cycles of herd 70-F-10 in September 1970, showing time intervals between animals entering each phase of the cycle.

Date	Interval Between Muskoxen Lying Down (min)		Time Between 1st & Last Down (min)	Time Down (min)		Interval Between Muskoxen Getting Up (min)		Time Between 1st & Last Up (min)
	range	mean		range	mean	range	mean	
12	0 -22	7.2	65	171-144	160	0 -33	5.4	49
13						1 - 7	3.2	30
13	1 -12	4.3	38					
14	0 -26	7.8	42	166-131	153	0 -23	3.2	30
15	0 -13	4.4	40	182-129	157	0 -13	3.6	32
15	0 -40	10.1	91	214-160	167	0 -12	4.1	37
17	0 - 9	3.3	30	194-165	181	0 - 4	1.7	15
21	0 -18	4.2	38					
27						0 - 5	2.1	19
29						0 - 3	1.4	13
	Means	5.9	49		164		3.1	28

periods of near-uniform length (Table 7).

The change-over time from feeding to resting-rumination was also variable but averaged about 45 min for a medium-sized herd (Table 6). The length of the change-over from resting-rumination to feeding was about 30 min.

In herds where all muskoxen were individually recognizable (eg. herd 69-A-4), times of individual feeding and resting-rumination periods were recorded. In other herds only resting-rumination periods could be recorded accurately for individuals. For feeding periods, only a value for the whole herd could be obtained.

During May, June and July, 1969, herd 69-A-4 was observed for 205 hours. The four animals in the herd could be individually recognized, mainly by horn size and shape, and were "named" as follows - "LB," the largest bull, with large, cracked and dark-coloured horn bosses; "2B," with symmetrical horn bosses, smaller and lighter than LB's; "1B," with asymmetrical horn bosses, lighter than 2B's; and "C," the cow, with typical adult female horns.

During May, June and July, 1969, 25 feeding periods and 19 resting-rumination periods were accurately timed for the four animals. (Other periods timed for only part of the herd were not included in the following analysis.) The mean durations of feeding and resting-rumination for each animal in

Table 7. The activity cycle of a herd of 7 muskoxen on June 13, 1968.

Time (CDT)	Herd Activity	Time Period (min)
1000	all feeding	126
1206	1st muskox down	
1210	all 7 down	4
	all resting/ruminating	51
1301	1st muskox up	
1307	all 7 up	5
	all feeding	155
1542	1st muskox down	
1602	all 7 down	25
	all resting/ruminating	75
1722	1st muskox up	
1735	all 7 up	13
	all feeding	188
2043	1st muskox down	
2120	all 7 down	37
	all resting/ruminating	140
2340	1st muskox up	
2400	all 7 up	20
	TOTAL	14 hours

the three months were as follows: for LB, 169.0 and 138.3 min; for 2B, 156.4 and 153.2 min; for 1B, 162.8 and 147.6 min; and for C, 175.0 and 132.5 min (Table 8).

The cow had consistently longer feeding periods and shorter resting-rumination periods than the bulls 2B and 1B but an analysis of variance conducted on the twenty-five feeding periods and the nineteen resting-rumination periods showed no significant difference between the four animals at the 5% probability level. However, the total feeding time for twenty-six periods for the cow is 80 hours, 18 min, and for 2B only 72 hours, 33 min, a difference of 7 hours and 45 min. The difference between the cow and 2B is not significant at the 5% probability level. There is no significant difference between the bulls 1B and 2B, nor between LB and the cow.

At the beginning and end of each feeding period, I noted the order in which the individuals commenced or finished feeding (Table 9). The cow and 1B were most often among the first two to rise (61.1%), but the dominant bull, LB, was most often the first (33.3%, Table 9a). The bulls 2B and 1B are most often the first to lie down (38.9 and 41.6%) and the cow, most often the last (36.1%, Table 9b). The cow and 1B were very seldom the last animal to rise (11.1%) and the cow was rarely the first one to lie down (5.6%).

Only occasionally were the activity cycles for two

Table 8. Duration of feeding and resting-rumination periods for the four muskoxen of herd 69-A-4 (LB, 2B, 1B, C) during May, June and July 1969.

Activity	Month	Mean Time (min)				No. of Periods
		LB	2B	1B	C	
Feeding	May	183.8	153.2	177.2	181.8	6
	June	162.1	148.1	151.4	166.2	14
	July	170.6	183.4	177.2	191.4	5
	mean	169.0	156.4	162.8	175.0	
Resting-Rumination	May	179.7	223.0	214.0	191.3	3
	June	137.5	151.1	147.0	131.9	11
	July	115.2	116.2	109.0	98.6	5
	mean	138.3	153.2	147.6	132.5	

Table 9. The order in which LB, 2B, 1B, C (69-A-4) began and ended feeding periods in the period May to July 1969 (expressed as a percentage).

(a) Beginning of feeding periods (n=36)

Muskox	First up	Second up	Third up	Fourth up
LB	33.3%	13.9%	25.0%	27.8%
2B	16.7%	16.7%	22.2%	44.4%
1B	30.6%	30.6%	27.8%	11.1%
C	22.2%	38.9%	27.8%	11.1%

(b) End of feeding periods (n=36)

Muskox	First down	Second down	Third down	Fourth down
LB	16.7%	25.0%	36.1%	22.2%
2B	38.9%	16.7%	30.6%	13.9%
1B	41.6%	27.8%	8.3%	22.2%
C	5.6%	33.3%	15.0%	36.1%

different herds in synchrony, and then only for short periods of time. In all herds observed the individuals within the herd had synchronized activity cycles. One exception involved the dominant bull of herd 70-E-15 who, over a period of days, gradually moved out of synchrony with his herd. Eventually he walked away from the others during his feeding period while the herd was just beginning the resting period. Several animals in the herd did stand up and watch him move away, turned to look at the others still lying down, and then resumed ruminating themselves.

On the other hand, the individuals in the few large herds or groups observed in February 1971 did not show this same synchrony. Rather, varying numbers of individuals would be feeding while others were resting and ruminating. For example, on 26 February, during four hours of observing two groups (12 and 27 muskoxen) at no time were all animals of either group up or down at the same time.

2. Contagious Behaviour

Contagious behaviour refers to the spreading of a behaviour pattern from one animal to another. The action of one animal stimulates or "causes" the same behaviour in others.

The most impressive example of contagious behaviour in muskoxen occurred during stampedes. If one animal broke

from a group defence formation, others would immediately follow. If one of the leading animals or one from the middle stopped and wheeled around after running some distance, the others would generally do the same. If a group split during a stampede, the group in front might stop and turn around but seeing the others run towards them, would again begin running themselves. This behaviour was observed to result in herds travelling over 5 km in less than 30 minutes on several occasions.

Another example of contagion occurred between the two phases of the activity cycle. At the end of a feeding period, as individuals lie down to ruminate, the interval between the first and last muskoxen to lie down was usually greater than the interval, at the end of the resting-rumination period, between the first and last to get up (Tables 5, 6, 7).

In comparing the variances in intervals between individuals when the herd 70-F-10 was lying down at the beginning, and when the herd was getting up at the end, of five resting-rumination periods (Table 6), the data were transformed by using $\sqrt{x + 1}$ to normalize the Poisson-distribution and tested using the F-test. A significant difference was found in one case ($F=5.916$, $p < 0.01$), but the other four showed no significant difference. In all of the examples tested, one animal, often the dominant bull, remained feeding or resting for a much longer time than the others and may have influenced these results.

The order in which each of 31 muskoxen (in a herd observed on 22 October, 1970) began a resting period was compared with the order in which they got up at the end using Spearman's coefficient of rank correlation. No significant correlation was found. When the order in which they began the resting period was compared with the amount of time spent lying down, a significant correlation was found ($t = 8.026$, $P<0.001$). In other words, the first animals to lie down were down longer than the last animals to lie down.

Contagion probably has an effect at both the beginning and the end of feeding periods but the action of an animal rising and walking slowly away probably has a greater contagious effect on a recumbent muskox than the lying down of a nearby animal has on another still feeding. Near the end of the feeding period there was a definite centripetal movement, only partly because the areas optimum for resting were somewhat restricted (at least in summer). At the beginning of a feeding period, the muskoxen spread out quickly and soon began moving away from the resting-rumination location in a centrifugal movement.

As the animals spread out, the frequency of social interactions was relatively high. Again at the end of feeding periods as individual distances gradually decreased, a higher frequency of social interactions was noted.

3. Herd Stability

Joining or splitting up of herds occurred at all times of the year (Appendix I). Some herds remained intact for only a few days before splitting and often a herd formed from the union of two small herds would split into different sized groups within 24 hours. However, other herds or groups remained intact for long periods of time. For example, the three bulls from herd 69-A-4 stayed together for 67 days (29 April to 5 July 1969). Three other examples of groups that remained together for similar periods of time, but as parts of several different herds, are taken from the August-October 1970 data (Appendix I, part 4). Four animals from herd 70-E-12, which formed on 9 September, remained together for 13 days following the splitting of the herd and were joined by 10 others for 7 days making a total of 69 days together. Five animals from the herd of 10 first seen on 6 September remained together for 58 days as part of 4 different herds.

The behaviour of the individuals and herds in these joining and splitting interactions will be discussed under Agonistic Behaviour.

The large "herds" seen in February 1971 showed much day-to-day fluctuation. These muskoxen were seen in groups of 10 to 53 animals with the average size of the group being about 40. The small herds of late winter and early spring

again showed the relative stability characteristic of summer herds.

4. Leadership

During the daily movements within a feeding area, muskox herds moved as loosely organized groups. In herd 69-A-4, the direction of movement while feeding was influenced by any of the individuals, with no single muskox remaining at the front of the herd longer than any other. In fact, the "front" of the herd often became the rear as individuals changed the direction of their movement.

However, during the periodic movements from one feeding area to another the herd usually travelled in single file and feeding activity was greatly reduced. In ten out of fifteen such movements recorded for herd 69-A-4, the bull, LB, initiated the movement and retained the lead position for most of the distance travelled. In two cases, he was not followed by the herd, but did return to them after some hesitation. Two movements were initiated by 1B but, after scent-marking displays by all three bulls, LB took over the lead position. The other bull, 2B, initiated one movement, was followed by the cow, watched by 1B and ignored by LB and eventually circled around and returned to the others. In two instances, after the herd size had increased to fifteen (i.e., herd 69-A-15), the whole herd moved off in one direction while LB moved off in

the opposite direction. The others gradually reversed their movement and again followed LB.

During such movements the order of travel in herd 69-A-4 was not constant. Often 1B or 2B would travel in front of LB for brief periods. Interactions such as head-butting and charging were common during some movements. When travelling, 1B and 2B interacted more often, and they and the cow stopped to feed more frequently than LB. Consequently, they often ran to catch up to LB who moved along at a steady rate.

In herds with few recognizable individuals, the influence of one particular bull on the movements of the herd was most evident when the herds were confronted by an obstacle such as a deep river or steep bank. Then after several herd members failed to find a route and remained standing or looking around, the "lead" bull would move up through the herd and continue on, sometimes trying several different routes before leading the herd past the obstacle.

Other instances of a particular bull behaving differently from the others and influencing the movements or behaviour of a herd occurred during attack by wolves or disturbance by man or machines. Leadership under these conditions will be described in later sections.

5. Discussion - Dynamics of the Herd

Neither Tener (1965) nor Harington (1961) described

the activity cycle of muskoxen. Bos (1967), from limited observations, suggested alternate feeding and resting periods of from .5 to 1.5 hours in duration. Stefansson (1924) indicated that muskoxen lie down for 2-3 hours after having filled up on vegetation.

In this study, the timing of the basic activity pattern of alternating 2½ hour periods of feeding and resting-rumination, was usually common to all individuals within a herd. This synchronization is not due to spatial considerations since, in the study area, grazing areas are relatively uniform and extensive enough that a herd does not have to search out a feeding place. Resting places, though somewhat restricted in summer, are also abundant. The length of feeding and rumination periods are doubtless influenced by general physiology and the quality of the food. Also, the weather or climate can affect the activity cycle by altering the time and energy necessary for muskoxen to obtain a suitable amount of food as well as altering the amount of food needed to maintain body processes. These variables over a long period of time would tend to act in opposition to the observed synchrony since individuals would not be affected in exactly the same way and would have feeding periods of different lengths.

The contagious aspects of behaviour, the influence of the behaviour or activity of one animal on others, are probably important in maintaining the synchrony of activity in the herds.

The effects of individual differences in length of feeding and resting-rumination periods within a herd may be balanced by the contagious aspects of behaviour. Individuals tend to do what others are doing, consequently the herd becomes synchronized.

The increase in social interactions as muskoxen rise and begin feeding following a resting-rumination period is probably due to the short distances between individuals before they spread out. The increase in interactions at the end of the feeding period also occurred when the individual distances were low as muskoxen moved towards those already lying down. This increase however, may also have been influenced by a decreased motivation for feeding.

Krämer (1969) found the opposite sort of movements between feeding and resting positions in chamois (Rupricapra rupricapra), with the individual distances increasing as more animals began the resting phase and decreasing as the feeding phase began.

The closeness of individual muskoxen and caribou while feeding in large herds led Hammel (1956) to suggest that the moisture cloud above such herds in winter reduces radiative heat loss to the clear sky. I doubt that this would have much effect on muskox herds, however, given the frequency of light to moderate winds. Although moisture clouds were seen near herds during very cold weather, the immediate drift away

from the herd was evident except on the rare calm days (recorded only 12 times in weather observations between November 1970 and March 1971).

The synchronization of activity patterns within a herd probably greatly increases the stability of the herd formation. Because of constant movement and wandering feeding habits, individuals that move out of synchrony with the herd would soon separate from the herd.

Herds were basically stable and, although break-ups occurred often, they almost always occurred following a disturbance, following the union of two herds, or when the large winter "herds" or groups split up into smaller herds in late spring. Break-ups at most times of year did not appear to be spontaneous.

The various possible connotations of the words lead, leader and leadership make the concept of leadership a complex one. To lead can mean to "go first," to "conduct, guide, especially by going in front of," or to "direct by example" or "direct movements of" (The Oxford English Dictionary, 1961).

Although many discussions of leadership in animals seem to use leadership only in terms of going first in a moving group of animals, I feel that a broader use of the term, to include the possible influence of one individual on the movements of a herd (where that individual may not always be

at the front of a herd), is necessary.

Stewart and Scott (1947) analyzed the reaction of pairs of goats (from a single herd) to human interference in order to determine what they called leadership. If the two goats moved away from the "disturber" together, the first to move was considered the leader if the other followed. This separation of a herd into pairs to determine leadership would surely create a situation in which leadership, as it applies to a herd of wild animals, could not exist.

Tener (1965) suggested that an older cow is usually the herd leader in muskoxen outside of the rut. He gave examples of such leadership only for a few situations where the herds were aware of, and disturbed by, his presence causing the herd to move away with the older cow moving at the front of the herd.

Under conditions of disturbance such as those imposed by Stewart and Scott (1947) and described by Tener (1965), the observed "leadership" does not seem to be the same phenomenon as that described under natural conditions in this study and by several other authors (eg., McHugh, 1958 and Geist, 1971). Rather, it may simply indicate that an individual who makes the first move is followed by the others. This could also be described as "followership."

Gilbert and Hailman (1966), in a study of leadership-

rank in fallow deer (Dama dama), found that when a group of does were frightened by approaching humans, they tended to follow a group "leader" in a linear sequence which became more variable as the leadership-rank decreased. No such sequence was noted for muskox herds in undisturbed or disturbed conditions.

Tener (1965) suggested that, during the rut, the dominant bull of a herd is the "decision-maker" in selecting feeding grounds or in reacting to danger. My own observations indicate that leadership in muskox herds is very closely related to the social dominance hierarchy not only during the rut, but throughout the year. This relationship between dominance and leadership will be discussed further in following sections.

III. MAINTENANCE BEHAVIOUR

A. Locomotion

The most common method of progression seen in the muskox was the slow diagonal (lateral sequence) walk. The footfall pattern was RH, RF, LH, LF. The head was lowest as each forefoot hit the ground, and swung slightly to the side of the falling forefoot. In this walk, an animal is able to stop suddenly at any phase without losing its balance (Bullock, 1971). The slow diagonal walk was used while feeding and moving within and between feeding areas.

When a muskox was disturbed the slow walk became a fast walk which abruptly shifted into a gallop. The gallop was seen in several circumstances including charging, clashing, chasing of cows by bulls, bulls being chased by dominant bulls and stampeding. The footfall pattern for the gallop was RH, LH, LF, RF., i.e. the lateral or rotary gallop pattern. In both field observation and preliminary analysis of a limited amount of 16 mm film, no gait intermediate between the walk and the gallop was noted.

When crossing rivers, muskoxen generally walked slowly and did not enter water deeper than chest height. In July 1968, an adult bull was seen crossing a flood-swollen river using a gallop-like gait which slowed to a rocking, surging motion creating a low wave in front. On

another occasion, a bull stepped into a river channel, sunk out of sight and was carried several meters downstream before he was able to reach shallow water and regain his footing. Muskoxen were not seen swimming during this study.

Another pattern of locomotion associated with water was observed in mid- and late summer. While the herd was feeding or travelling, a single cow or bull walked out into the middle of a shallow pond, stood briefly, then began whirling around, jumping and splashing and flinging the head up and down. I observed this behaviour being performed by cows on three occasions and by adult bulls 10 times. This behaviour is very similar to the patterns of play behaviour shown by muskox calves (Tener, 1965).

When travelling in deep snow, as for example when crossing a river channel or climbing a lee drift at the foot of a hill, muskoxen moved in single file with each animal, regardless of size, sex or age, placing each foot in the footprints made by the lead animal. Muskoxen often followed in tracks made by other herds or, in some cases, by humans.

B. Stances

Several different postures or positions were assumed by muskoxen during the resting-rumination phases of the daily activity cycle. Two distinct postures were seen while the animals were lying down ruminating. In the first, the hind

legs were folded underneath, the forelegs were either folded backwards under the body or one was stretched out in front, and the head remained upright, with the muzzle near the ground (Figure 10). In the second rumination posture the head was lowered and stretched out in front, with the chin resting on the ground or a foreleg. In both positions, the fore-part of the body remained vertical.

In other postures associated with rest, the chewing movements of rumination could not be seen. In the basic non-ruminating position, the sprawl, muskoxen lay on their side with the legs extended out from the body. The sprawl was often modified by leaning against a snow-drift in winter and by lying against a hummock or ice-mound in summer.

During storms, muskoxen lay with their backs or sides to the wind. No evidence of huddling or standing in a group facing the wind was seen, even in winter storms. For example, on 9 February 1971, during winds of 24 knots (12.5m/sec) with blowing snow and temperatures of -27 F (-32.8 C), muskoxen continued to feed in the usual manner or remained lying down.

Before rising from the sprawl position, muskoxen often rubbed the shoulder hump and back against the ground and rolled onto the back briefly, waving the legs in the air.

Muskoxen usually assumed the upright rumination position briefly before rising. Normally, the hind legs were ex-

tended first followed by extension of the forelegs. However, as Tener (1965) has described, sometimes the muskox extended the forelegs first and remained in a "sitting" position for a short period of time before rising (Figure 11).

After rising, muskoxen stretched in the usual mammalian fashion by extending the head and neck, straightening the legs and raising the shoulders. I have not seen muskoxen extend and stretch the legs individually as has been reported for mountain goats (*Oreamnos americanus*) by DeBock (1970) and mountain sheep (*Ovis*) by Geist (1971). A yawn generally followed or accompanied the stretch.

During the time of heavy shedding and after a rain or snow storm, muskoxen shook briefly after rising. The shaking movement started at the head and progressed down the body quickly.

There was no special posture associated with defecation and it was often difficult to ascertain when defecation had occurred. Muskoxen sometimes defecated while moving in winter, when the faeces are expelled in the form of compact pellets but in summer, they more often defecated while standing. Muskoxen often rose and defecated during a resting-rumination period and usually defecated after rising, before beginning to feed.

Urination usually accompanied defecation and thus

Figure 10 Adult bull muskox in typical rumination posture.

Figure 11 Adult bull muskox in "sitting" position after rising from rumination position by straightening forelegs.

often occurred at the end of the resting period. Urination was much easier to detect as there is a particular urination posture which differs between males and females. The female urination posture is characterized by a hunched back, hind-quarters depressed slightly and the hind legs slightly spread (Figure 12a). The male urination posture is similar to the stretch, which it often follows, except in that the position of the head is lower (Figure 12b).

When muskoxen rose to defecate or urinate during a resting-rumination period, they often moved a short distance and spent a few minutes choosing a new location before lying down again. In four resting-rumination periods of herd 69-A-4, the total time the four animals spent in a standing position amounted to only 4% of the total period.

When a cow or bull was visually investigating an unfamiliar or new object such as a nearby herd, a wolf or a human, the head was raised to a position higher than at any other time except during a stretch. This "attention" posture was usually of a much longer duration than the stretch, the ears were directed forward and the nose was lifted frequently as the wind was tested for scent. A sudden lifting of the head occurred when the presence of a predator or human seemed to be first detected and may be considered an "alarm" reaction (Figure 13).

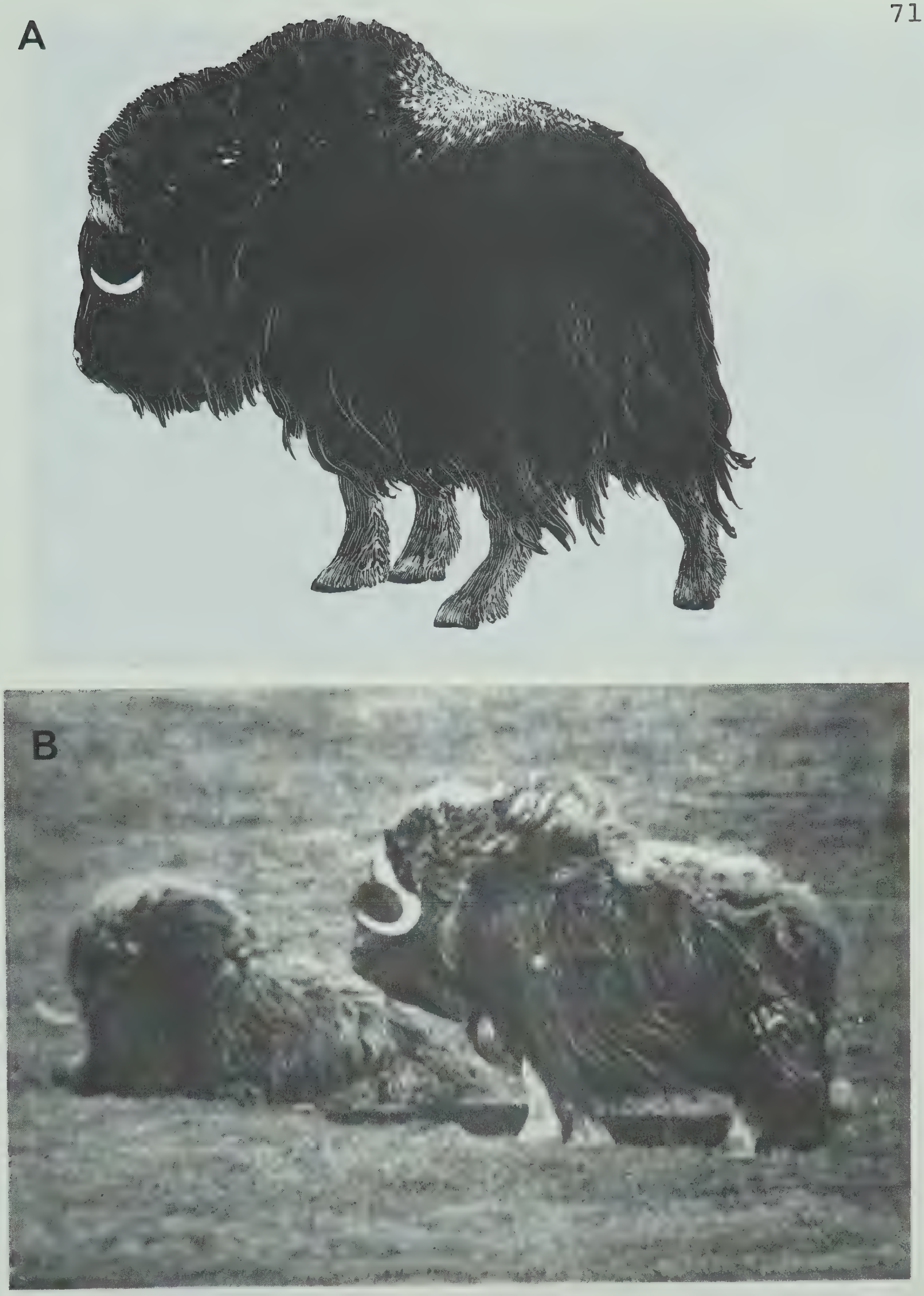


Figure 12 Muskox urination postures, A - adult female, B - adult male.

Figure 13 Adult bull muskoxen with heads raised in the alarm position upon meeting the observer at close range.

C. Grooming

Care of the body surface (grooming) was reduced in muskoxen compared to other ungulates. Excluding rubbing while in the sprawl position and shaking after rising, only 26 observations of grooming behaviour were recorded during this study (Table 10). The most frequently observed grooming behaviour was rubbing the body against the substrate or other individuals. Scratching with the hind legs was observed only nine times and licking of the body surface was never observed. Most grooming occurred during the summer when the underwool was being shed.

D. Drinking and Feeding

Muskoxen were observed drinking water from ponds and shallow lakes on only nine occasions.

The manner in which muskoxen feed and the plant species utilized have been described by Bruggemann (1953, 1954), Tener (1965) and Bos (1967) among others. Noteworthy is the continuous movement and the fact that the head is held low to the ground even when the muskox is moving between feeding places.

The action described by Tener (presumably for the mainland sub-species) in which the tongue is wrapped around the vegetation was not seen. Rather, the grasses and sedges were grazed by using the lower incisors against the upper pad and by pulling with the head. When feeding on the arctic

Table 10. Number and timing of observations of several types of rubbing actions (both grooming and non-grooming) in non-social situations (1968-1971)

Circumstances	Grooming (No. of occurences)	Non-grooming Rubbing
Substrate Used:		
- snow	3	16
- hummock	1	8
- ground	4	
- gully	5	
Part of Body Scratching with:		
- foreleg	1	
- hindleg	9	
Scratching at:		
- belly	2	
- head	2	
- foreleg	4	
Rubbing with:		
- head		24
- horns		13
- preorbital gland		8
Timing:		
Immediately		
- after rising	5	5
- before lying down	7	4
Within 15 minutes		
- of rising	3	10
- of lying down	2	8
Total No. of Actions	26	32

willows this pulling was quite distinctive. A repeated, sharp, upward movement was used to pull up and break off the outer twigs.

In winter, several different patterns of removing the snow cover before feeding were seen. A light snow cover was removed from the vegetation by pushing with the nose. In deeper or harder snow, the forefeet were used. Right and left forefeet were used alternately and the pawing motion pushed the snow back and to one side. For example, on 18 November, 1970, at a temperature of -10 F (-23.3 C) to -23 F (-30.6 C), a herd of five muskoxen were feeding in soft snow, about 23 cm deep with a light crust. An adult bull during a 20 minute period spent 18 minutes feeding in five feeding bouts (mean = 3.6 min). Overall, the number of pawing motions averaged 2.8 per minute or 9.8 per feeding bout. The average number of pawing motions for each foreleg before alternating was 2.5, with feeding occurring before alternating. Between feeding bouts the muskox generally moved several meters to either undisturbed snow or an area already cratered during that or the previous day. A crust thick enough to support a man's weight (4 to 8 cm) was broken, once an edge had been established by pawing, by a lifting and dropping motion of the head. The impact of the chin on the crust broke free chunks of snow up to 1.8 m^2 in size.

E. Discussion - Maintenance Behaviour

The method of locomotion used most often by muskoxen is a key part of the stolid, "phlegmatic" muskox way of life. The slow, stable walk is used while feeding and when moving through and between feeding areas.

Harington (1961), presumably on the basis of his own observations, stated that muskoxen cannot trot. My own observations support his conclusion but further analysis of muskox locomotory patterns is desirable.

The frequency of the use of the gallop and the lack of the trot, make the muskox an obvious exception to the statement by Dagg and de Vos (1968) that animals with heavy antlers or horns use the symmetrical trot more frequently than the gallop. They pointed out that the center of gravity changes less radically in the trot and suggested that control of the heavy head is easier in the trot than in the gallop. They also suggested that galloping requires less energy for moderate-sized animals than for heavy ones, mainly because all of the animal's weight must be launched into a period of suspension from one foot. The absence of trotting in muskoxen may be partially due to the nature of the ground surface. Small hummocks, frost cracks, patterned ground and felsenmeer would all tend to discourage use of a symmetrical gait such as the trot, as would the great variability of snow conditions in winter.

Pedersen (1958) reported that muskoxen assume a tightly-grouped position during winter storms with adult bulls forming the apex of a wedge facing the wind. In this way, he suggested, calves are protected by the wall of bodies. However, I find his interpretation questionable and suggest that if he was close enough to see the herds under such stormy conditions, he may well have been the cause of the grouping. My own observations of muskoxen in storms suggest that a resting position is probably more effective in preventing heat loss than standing in a group. The wind would certainly blow through the herd at ground level and affect the shorter calves even in a very tight group. The relatively poorly insulated legs are protected while lying down and presumably calves could lie in the lee of the mother for adequate protection.

There are reports in the literature (see Hone, 1934, Harington 1961) of muskox "sentries" standing on the lookout while the herd rests. The basis of these reports is very likely a muskox rising to defecate and urinate during a resting period. Such an animal, especially a bull in the urination posture, could easily give the impression of a watchful sentry to someone observing a herd for a short period of time.

The very noticeable lack of grooming behaviour in muskoxen is probably related to the lack of external parasites. Tener (1965) reported no external parasites and my own obser-

vations of several living (drugged) animals and fresh (wolf-killed) carcasses have confirmed this (Samuel and Gray, in prep.). Hence, the only "foreign" matter to be groomed from the coat is the wool shed each summer, along with bits of plant material caught in the wool.

The very limited number of observations of muskoxen drinking free water suggests that in summer, enough moisture is obtained when feeding in wet areas and from the vegetation itself, and in winter by ingesting snow along with the plant material.

The pawing of feeding craters is a stereotyped and repetitive motion. However, this stereotypy and repetitive nature are not sufficient to fulfill the criteria of a consummatory act as Pruitt (1969) has suggested for such pawing in caribou. Pawing in muskoxen and probably in caribou also is only stereotyped in that for a given snow cover, a certain method of pawing is likely the most effective way of clearing snow from the vegetation. As long as it is effective, there is no reason to expect variability.

This method of feeding in which craters are dug in the snow is of great importance in relation to social behaviour as will be discussed in the following section.

IV. SOCIAL BEHAVIOUR

A. Agonistic Behaviour

Under the heading "agonistic behaviour," I refer to any behaviour that is connected with a contest or conflict between two animals (after Scott, 1958). The following behaviour patterns were performed by muskoxen in agonistic interactions.

1. Description of Behaviour Patterns

Displacement from feeding crater (D). Displacements generally occurred while herds were feeding in snow and consisted of one animal walking towards another and displacing it from a feeding crater. Usually, the displacer approached from behind and no actual contact was made. The displaced animal normally walked ahead but occasionally ran for a short distance.

Butting (B). After displacements, butting was the most common of the agonistic social interactions. In butting, one bull approached another usually with a short run or at a walk from a short distance and delivered a blow with the horn base upon the horn boss of the opponent. There may be an obvious initiator or both interactants may move simultaneously. After contact, pushing or rocking back and forth, with horn bosses together may occur (Figure 14).

Charging (C). Charging is very similar to butting and my division between them is an arbitrary one based on the

Figure 14 Two adult bull muskoxen pushing head-to-head after a butting interaction.

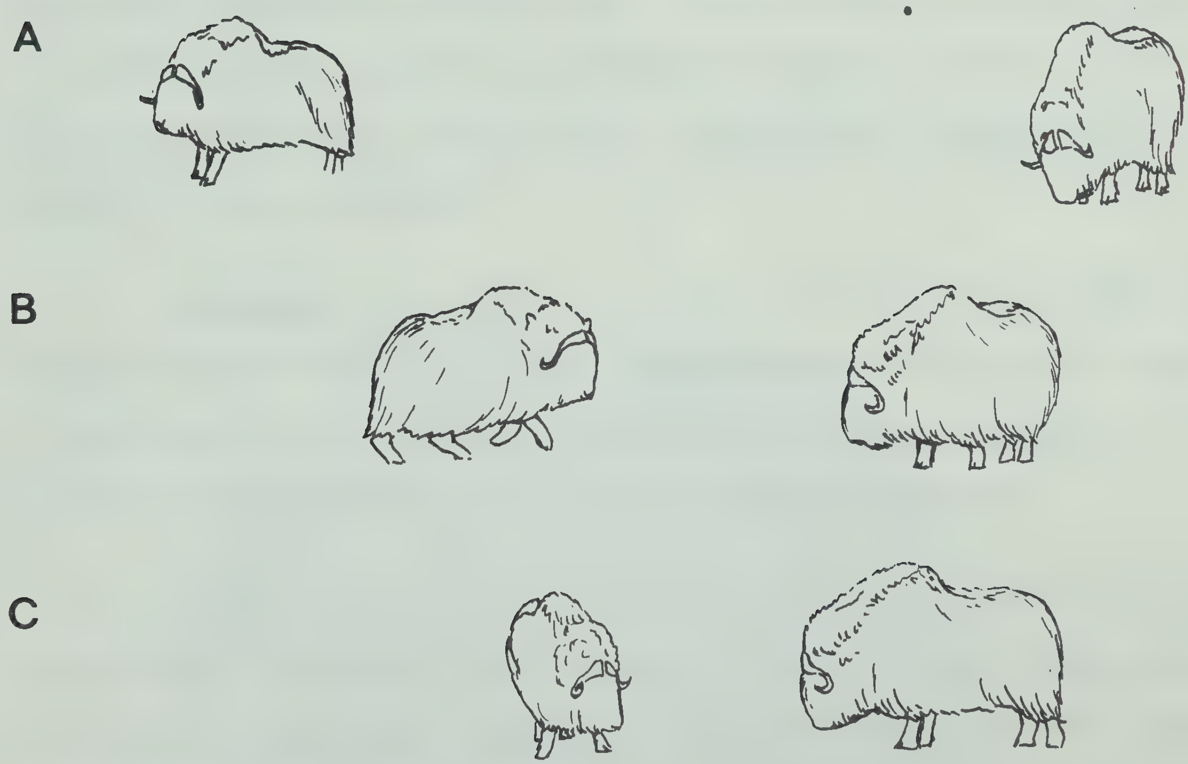


Figure 15 Subadult bull muskox charging a dominant adult bull. (A) Subordinate bull (left) begins charge as dominant bull still feeding, (B) Subordinate bull charges as dominant bull lifts head, and (C) Subordinate bull jumps back quickly after impact.

distance the initiator runs before impact. If one of the two bulls galloped for 9 m or more before colliding head-on with the other, the interaction was considered a charge rather than a butt (Figure 15). Simultaneous charges by both interactants were rare. Only in clash-type interactions did more than one charge occur in sequence.

Head-up (H-up). In the head-up posture the muskox stood with the head raised, facing the individual with which he was interacting (Figure 16). This posture was also seen in male-female courtship interactions and I distinguish it from the attention posture only through the circumstances in which it was performed.

Rubbing (R). Rubbing refers to a behaviour shown by both cows and bulls in which the preorbital gland and surrounding area of the head were rubbed against the substrate, i.e., rocks, small hummocks, or hard-crusted snowdrifts.

Gland-rubbing (G.R.) In gland-rubbing behaviour, a cow or bull extended one foreleg in front of the other, placed the preorbital gland against the inside of the leg and rubbed the head up and down against the leg (Figure 17). The up and down rubbing motion was usually repeated two or three times, then that foreleg was retracted and the other extended and the rubbing repeated on the other leg. Examination of slow motion 16 mm film shows that the rubbing action was slowest and most

Figure 16 Adult bull muskox in the head-up position.

Figure 17 Adult bull muskox gland-rubbing.

forceful at the point where the gland itself was against the leg. The movement of the head pushed the foreleg down so that only the back of the hoof and the dew-claws rested on the ground. The motion was speeded up and the pressure decreased as the lower part of the face was rubbed against the leg.

Horning (H). During some agonistic encounters, bulls rubbed the horn bosses against the ground and vigorously dug at and tore into the ground, sides of hummocks or gullies with the horn tips (Figure 18).

Pawing (P). A brief pawing motion of the foreleg, with scraping of the ground, occurred in a few interactions. Digging of pits in the soil (Tener 1961, 1965) was not seen.

Head-Tilt (H.T.) The head-tilt is a broad display in which one bull moves in front of and around another in a slow, stiff-legged walk. The head was tilted so that the nose was held away from recipient and the horn boss was directed towards him. The mane appeared to be erected and the motion of the displaying bull was such that he moved almost sideways, with the shoulder leading as he circled around another individual (Figure 19).

Parallel Walk. If two interacting bulls performed the head-tilt display simultaneously, circling no longer occurred and the two walked parallel to each other and in the

Figure 18 Adult bull muskox (A) and subadult bull muskox (B) horning the ground.

A. Adult bull horning the ground, using the tips of the horn to dig at the flat surface,

B. Subadult bull (left) rubs the face and boss of the horns against the ground and, while rubbing and gland-rubbing, catches his horn behind his foreleg (right).

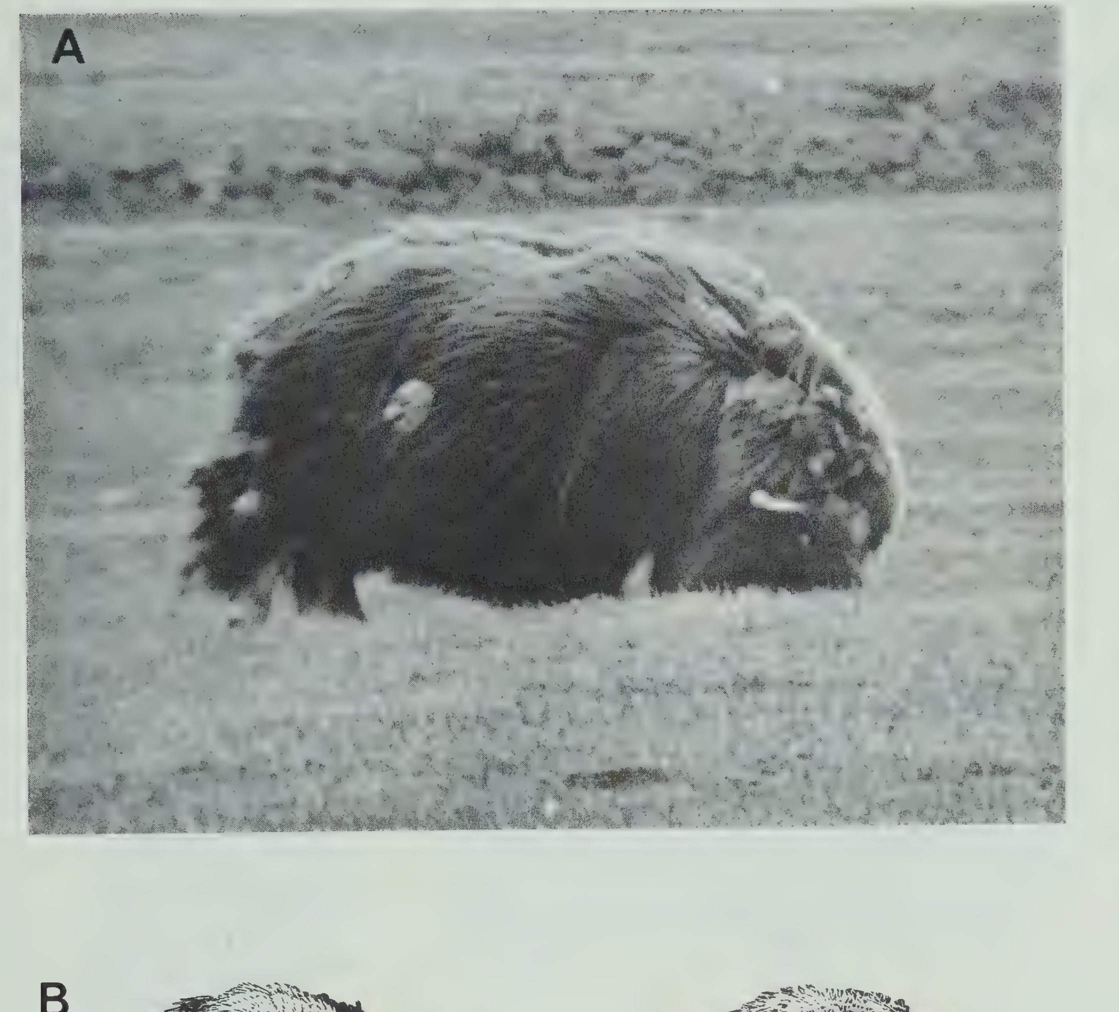
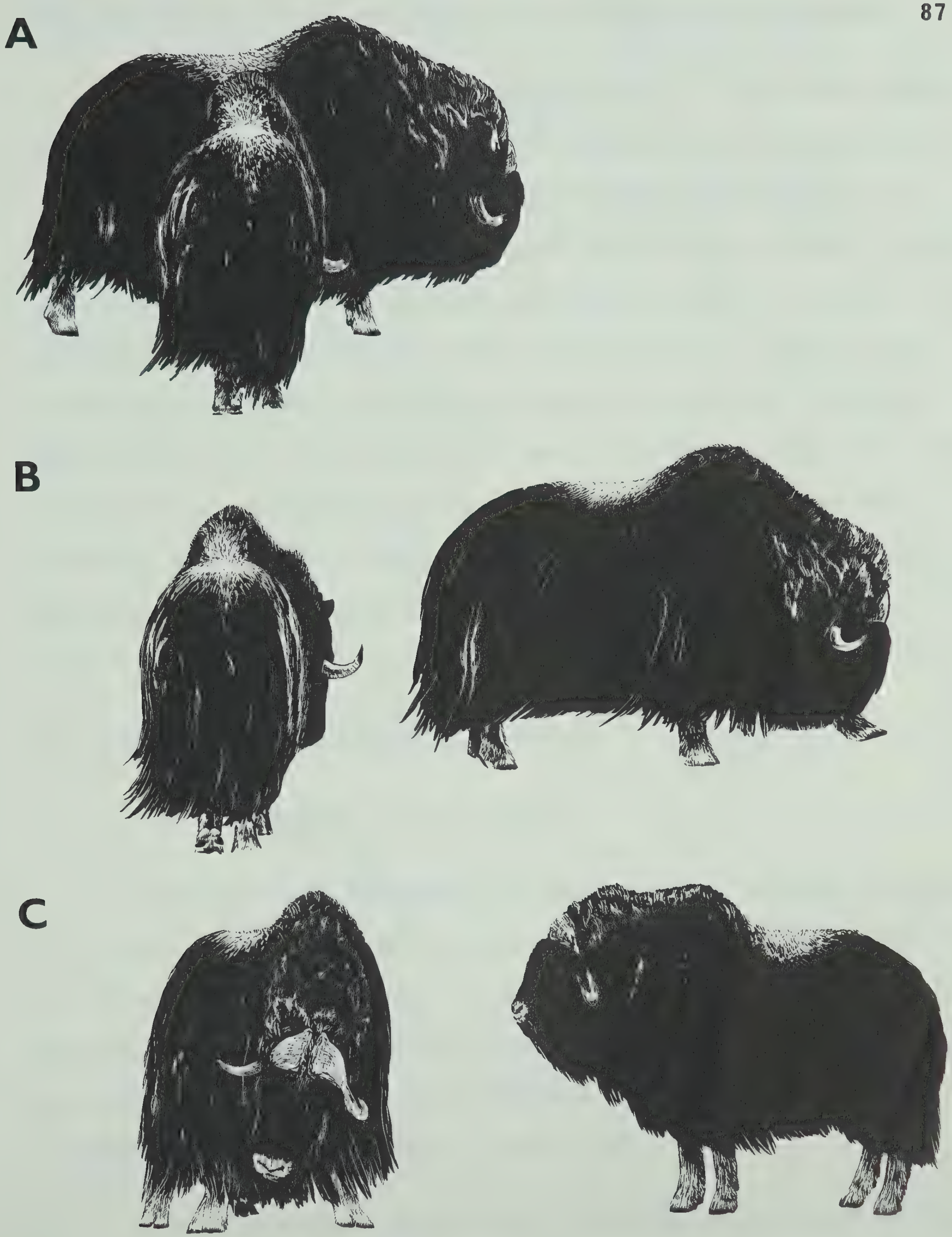

A
B

Figure 19 The head-tilt display.

A. - dominant bull head-tilting to subordinate bull (in foreground),

B. - dominant bull gland-rubbing after head-tilting around the subordinate, in foreground (same interaction as A),

C. - adult bull head-tilting to other adult in head-up position (right).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C

same direction, with the same slow exaggerated movements.

Clash (Cl) and Headswinging (H.S.). The clash seems to be a further development of the patterns of butting and charging. In all clashes, both bulls charged forward at a gallop and met with the full impact on the horn bosses (Figure 20). The clashing was usually preceded by gland-rubbing, head-tilting or other agonistic behaviour patterns. Before each charge of the clash, both bulls backed up slowly, swinging their heads back and forth in a deep, wagging motion with the head held up slightly and the muzzle tucked in toward the chest (H.S.). The headswings were in time with the footfall pattern. After several charges, the bulls may engage in a head to head pushing contest.

2. Intraspecific agonistic behaviour

a. Behaviour within herds

The overall frequency of interactions between members of a herd of muskoxen was comparatively low. During most of the feeding period and all of the resting-rumination period, few overt interactions were recorded. The exception to this was when the ground was snow-covered and displacement-type interactions became frequent (Table 11).

Displacement interactions recorded during this study indicated that adult bulls displaced cows and cows never displaced adult bulls, adult bulls displaced subadult bulls, and

Figure 20 A clash between two adult bull muskoxen from the same herd, 12 July 1968.

A. Two adult bulls horning ground; adult cow (right) and other adult bull (foreground) watching,

B. The two bulls begin backing up and head-swinging,

C. The bull on the left stops, the other continues to back up,

D. The bull on the right begins the charge,

E. Both bulls charging forward,

F. After impact both bulls push head-to-head,

G. The bull on the right pushes the other steadily backwards. The cow runs towards the combatants,

H. The bull on the left runs away, the cow approaches the other bull and the third bull remains standing but looks away.

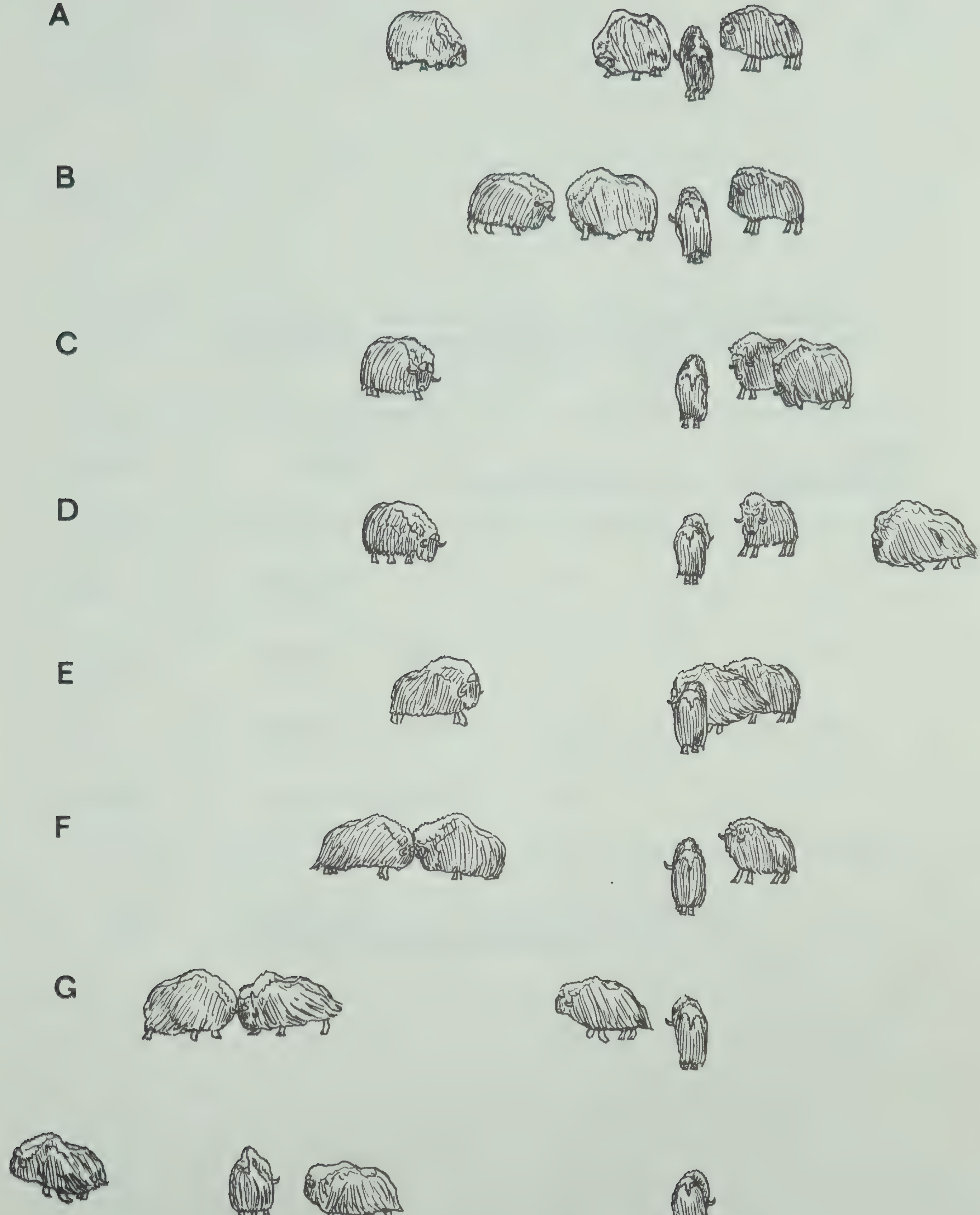
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Table 11. Numbers of displacements from feeding craters recorded for two muskox herds in the period May to August 1968.

Month	Herds	Total Displacements	No. of "days"* Observations
May	68-A-11	79	5
June	68-A-7, 68-B-5	74	19
July	68-A-7, 68-B-5	21	16
August	68-B-6, 68-B-7	3	7

* "day" = approximately 3 hours observations during feeding activity.

subadult bulls could displace cows and vice versa (Tables 12 to 15).

Frequently when one muskox displaced another, the individual displaced, in turn displaced a third animal. These chain-reaction type interactions involved up to five displacements and in each case, the animals toward the end of the "chain" never displaced those involved earlier in the same chain. These observations suggested that displacement depended not only on the social class of the individual but also on its social "status" within that class. Also, different individuals which appeared to be in the same social class (i.e., adult bulls) reacted in different ways to certain other behaviour patterns performed by another individual of the same class.

Analysis of displacements recorded for a particular herd showed that the number of times an individual was displaced was not due to chance but was related to the number of individuals in that herd belonging to each of the social classes. For example in analyzing the displacement interactions of herd 69-B-9, if it is assumed that social class does not affect the frequency of displacements, the expected numbers of displacements are significantly different from the observed for adult muskoxen (Table 13a). If, however, it is assumed that social class does affect frequency of displacements, then the expected and observed numbers of interactions are not

Table 12. Total number and types of displacements occuring during feeding, recorded from May 1970 to May 1971.

Month	Bull displaces cow	Bull displaces bull	Cow displaces cow	
May 1970	149	71	89	
Sept. 1970	8	3	8	
Oct. 1970	41	4	30	
Nov. 1970	36	32	10	
May 1971	33	85	3	
TOTALS:	267	195	140	= 602

Month	Total Displacements	Displacing M.* uses crater	Displacing M. doesn't use crater	Displaced M. digs new crater	Displaced M. uses old crater
May 1970	309	165	90	137	54
Sept. 1970	19	4	2	1	0
Oct. 1970	75	43	17	8	0
Nov. 1970	78	38	26	29	7
May 1971	121	23	41	19	23
TOTALS:	602	273	176	194	84

* M. = Muskox

Table 13. Observed and expected frequencies of displacements from feeding craters in herd 69-B-9 (7 adult bulls, 1 subadult bull and 1 cow) in May 1969.

	expected	observed	difference significant at* p=.01	.05	.10
(a) Assuming social class does not influence numbers of displacements (n=76)					
No. of displacements involving all 7 adult bulls	59.1	72	-	-	yes
- as displacing muskox	29.6	47	yes		
- as displaced muskox	29.6	25	-	-	-
No. of displacements involving YB**	8.4	8	-	-	-
- as displacing muskox	4.2	4	-	-	-
- as displaced muskox	4.2	4	-	-	-
No. of displacements involving cow	8.4	22	yes		
- as displacing muskox	4.0	0	-	yes	
- as displaced muskox	4.2	22	yes		
(b) Assuming social class does influence number of displacements (n=76)	expected	observed			
Adult bulls displace cow	14.8	18	-	-	-
All bulls displace cow	16.9	22	-	-	-
Adult bulls displace adult bulls	44.3	50	-	-	-
All bulls displace all bulls	59.1	54	-	-	-
Adult bulls displace YB	12.5	4	-	yes	
Subadult bull (YB) displaces cow	2.1	4	-	-	-

* Goodness of fit tested using X^2 (G-test for numbers less than 5). **YB=Subadult bull

significantly different for adults (Table 13b).

(i) The Dominance Hierarchy. The first opportunity to determine how the observed differences in reaction and frequency of interactions between and among social classes might be related to a social dominance system came when the individuals in herd 68-A-7 began shedding their wool. The different shedding patterns provided a reference point for distinguishing individual differences in the shape and size of the horns, permitting individual recognition of all five bulls.

Unfortunately, this herd remained in the study area only one week and the recorded number of interactions between known individuals was therefore very small (Table 14), but did indicate a linear dominance system among the bulls.

A second and more productive opportunity to investigate the social dominance structure came in 1969 when herd 69-A-4 (3 bulls, 1 cow) was observed for 205 hours during May, June and July.

Because the four individuals in this herd could be identified easily and because the herd was accessible for such a long period of time, conditions were almost ideal for determining the presence or absence of a dominance hierarchy and its nature, if one were present.

The three types of interactions I used initially in

Table 14. The dominance hierarchy in Herd 68-A-7 (5 bulls, 2 cows) in June, 1968.

	CB	TB	BL	FB	DC	WC	YB	TOTAL
CB dominates	-	0	3	1	1	1	0	6
TB dominates		-	4	1	1	1	0	7
BL dominates			-	1	0	0	2	3
FB dominates				-	0	1	1	2
DC dominates					-	0	1	1
WC dominates						-	1	1
YB* dominates						1	-	1

* YB - subadult bull

Table 15. The dominance hierarchy in Herd 69-A-4 during the summer of 1969.

(a) Dominance based on 241 displacements.

	LB	2B	1B	C	TOTAL
LB displaces	-	42	21	30	93
2B displaces	0	-	29	63	92
1B displaces	0	1	-	55	56
C displaces	0	0	0	-	0

(b) Dominance based on butting, charging and displacements. (281 interactions)

	LB	2B	1B	C	TOTAL
LB dominates	-	49	23	30	102
2B dominates	0	-	56	63	119
1B dominates	0	5	-	55	60
C dominates	0	0	0	-	0

determining the dominance system were displacements, butting and charging. For 241 displacement interactions, LB was the displacing animal in 100% of 93 interactions, 2B in 68% of 135 interactions and 1B in 53% of 106, whereas the cow was displaced in all 148 interactions in which she was involved (Table 15).

In determining dominance from butting and charging interactions, if a muskox ran from an encounter or turned aside quickly, I interpreted this as a "loss." A "win" was awarded to an animal that stood while the other ran or that turned aside slowly and began moving or feeding in the usual manner. The outcome was tabulated as inconclusive if, after the interaction, both animals moved away simultaneously or if both stood and began feeding.

When all three types of interactions were considered (Table 16), LB "won" 100% of those interactions (with a known outcome) in which he was involved. The bulls 2B and 1B "won" 68.9% and 43.2% respectively. The cow "lost" all interactions she took part in. If only the interactions between the three bulls are considered and inconclusive and unknown results are included in the total interactions for each bull (Table 16), the percentage of "wins" for LB is 93.5%; for 2B, 40.9%; and for 1B, 4.5%. The greatest number of inconclusive results occurred between 2B and 1B (17.7%).

Table 16. Social interactions between the three bulls LB, 2B and 1B of herd 69-A-4 during the summer of 1969, showing initiator and winner of the interactions.

Muskoxen	D*	B	C	Total	Initiator	D	B	C	Total	Winner	D	B	C	Total
LB + 2B	42	7	3	52	LB	42	3	-	45/52	LB	42	5	2	49/52
					2B	-	1	3	4/52	2B	-	-	-	0/52
LB + 1B	21	4	-	25	LB	21	2	-	23/25	LB	21	2	-	23/25
					1B	-	-	-	0/25	1B	-	-	-	0/25
2B + 1B	30	49	7	85	2B	29	16	3	48/85	2B	29	25	2	56/85
					1B	-	17	4	21/85	1B	1	3	1	5/85

Results: LB+2B - "Conclusive"- 49/52, "Inconclusive"- 0/52, "Unknown"- 3/52

LB+1B - " 23/25 " 1/25 " 1/25

2B+1B - " 61/85 " 15/85 " 9/85

LB "won" 72 out of 77 interactions = 93.5%

2B " 56 " " 137 " = 40.9%

1B " 5 " " 110 " = 4.5%

* D = Displacements

B = Butts

C = Charges

Although I have used only three behaviour patterns in determining the social dominance structure in a particular muskox herd, other agonistic behaviour patterns are very closely related to this dominance structure. The following sections deal with all of these patterns as they relate to social behaviour and the social structure of a herd.

Displacements. During certain observation periods, as well as recording the number and frequency of displacements and the individual involved, I also recorded whether or not the displacing muskox used the crater already dug, and whether the displaced muskox moved to a new area or returned to an area previously cratered (Table 12). During snowy or foggy weather and when the snow cover was soft or shallow it was difficult to see what each animal did during a displacing action. Therefore, many displacements were recorded without all the above information on use of old or new craters. The number of displacing actions decreased rapidly as the muskoxen began feeding in snow-free areas in late May and early June. Also, during the period of September-October, when the snow cover was light, very few displacements occurred. The total observation time per month varied and observations on several different herds were included.

Bulls displaced cows in 44% and other bulls in 42% of the total displacements (Table 12). The displacing muskox used the vacated crater in 61% of the known interactions (n = 449).

When only bull-bull interactions (n = 130) are considered, the feeding crater is used by the displacing bull only 44% of the time. Displaced muskoxen moved to a new area in 70% of the interactions (n = 278) and returned to a previously cratered area 30% of the time. (Here, "previously cratered" refers to the same day or the preceding day only.) In bull-bull interactions only (n = 80), a new area was used 55% of the time.

Butting and Charging. The following analysis of butting and charging between bulls excludes those interactions recorded during or immediately after a disturbance or union of two herds, during a more prolonged and intensive interaction (such as those including head-tilt displays or clashing) and the interactions between the three bulls of herd 69-A-4.

In 83 interactions, 82 butts were recorded. In 15 interactions, both butts and charges occurred and in 5, only charges occurred. For 14 charges the initiator of both the charge and the whole interaction were known. In 9 of these 14 charges, the original initiator of the interaction initiated the charge; in 2, the original recipient initiated the charge; and, in 3, both charged simultaneously. The initiator won 21 of 32 charges for which a winner was determined. In these short interactions, never more than 2 charges or 3 butts occurred per interaction. The occurrence of associated behaviour patterns, such as rubbing, pawing and horning, was low

and could not be associated with known relative dominance. The sequence of events was quite variable with no one sequential pattern occurring more frequently than any other.

Scent-marking. The use of a specialized motor pattern to deposit chemical signals originating in urine, faeces, or cutaneous scent glands on objects in the environment or on other animals of the same species is termed scent-marking (Ralls, 1971). I consider also the pattern of depositing scent on part of the animal itself (as is the case for musk-oxen) to be a type of scent-marking.

The patterns of rubbing and gland-rubbing are essentially the same motor pattern and were often seen in close temporal proximity. Rubbing and gland-rubbing were observed in many different circumstances, most of which could be considered to have an "aggressive" element. They occurred as the major single component of bull-bull interactions (Table 17), as a component of within-herd interactions involving head-tilt and other displays, as part of display encounters between bulls from different herds and one or the other occurred in virtually all instances where herds or solitary animals were disturbed by man, noise, machines or by other species. In other cases, these two patterns appeared directly before or after resting periods (Table 10).

Although many cases of rubbing occurred in non-encounter

Table 17. Interactions between bulls in which gland-rubbing (by only one of the bulls) was the major component.

	Initiator	Recipient
Encounters with:		
Gland-rubbing	6	0
Rubbing	3	1
Horning	1	1
Pawing	1	1
Facing other	1	2
Ignoring other	0	0
Watching other, head-up	0	2
Encounter ending with:		
One departing quickly	0	4
Charge or Clash	0	0

situations and were not associated with any of the agonistic patterns to any high degree, in some instances, scent-marking or rubbing the preorbital gland on a specific object of the substrate was followed by scent-marking by a second individual from the same herd on the exact location of the first. Both horning and gland-rubbing accompanied many of these bouts of rubbing.

Twenty-seven bouts of this type of marking were observed, 12 of these being the original marking by the first animal and 15 the marking of the second, third or fourth muskox. Eight bouts involved only two muskoxen, two involved three and two involved four animals marking the same location in turn (Table 18).

Of 12 original rubbing bouts, 9 initiated an interaction (i.e., no behaviour pattern other than "normal" walking or feeding was noticed prior to the rubbing), 2 followed gland-rubbing and 1 followed a butt. In 15 cases of a second animal marking a previously marked location, 5 followed the previous scent-marking directly, 5 followed horning by the previous marker (with all 5 horning bouts following the preceding marking directly), 3 followed gland-rubbing by the previous marker and 1 each followed a butt and gland-rubbing by the second animal.

Of 12 cases in which the relative social status (social class or dominance rank within a class) of the interactants was

Table 18. The sequence of behaviour patterns shown in scent-marking interactions involving more than one animal marking the same location

Individual Involved*	Object Rubbed			Other Behaviours Shown**				
	Snow	Hummock	Ground	G.R.	Paw.	Horn.	Butt.	H.T.
1B	2***					3	1	
OB	4					5		
1B		1						
2B		2						
YB		3						
C		4						
B			1	2				
TB			3	6	4	5		
3B			7	8				
TB			1			2		
LB			3	5		4		
B		1				2		
C		3				4		
2B		3		2			5	1
1B		4						
LB			3	2	4		5	
SB							1	
LB		1		4	3	2		
YB		6		9	7	8	5	
2B	1							
C	2							
YB			1			2		
HB			3					
1B	1							
2B						3		
LB	3							
LB		1						
3B							2,6	
2B		4		3			5	
C				7				
Total	3	5	4	6	3	7	5	1

* B = Bull, C = Cow, YB = Subadult Bull
** G.R. = Gland-rubbing, H.T. = Head-tilting
*** Numbers indicate sequence of patterns.

known, the dominant animal marked first in 11. Gland-rubbing accompanied 12 of 27 individual marking or rubbing bouts, pawing accompanied 4, and horning 11.

In two of the above interactions the involvement of olfaction is additionally demonstrated by the observation of a second animal sniffing at the object marked by the first and by another observation of a second animal turning abruptly from his direction of movement to approach the marked location.

Two additional examples of situations in which several individuals scent-marked the same location are discussed under behaviour between herds.

Mutual rubbing of preorbital glands by two individuals was rare. On 17 May 1970, a subadult bull moved up to a mature bull, they butted together gently then rubbed each other's muzzles. The mature bull turned away from the younger. On another occasion (herd 68-A-7), the dominant bull TB head-tilted to BL, gland-rubbed, then BL moved forward to butt with TB. Then BL rubbed his muzzle against the area of TB's preorbital gland. After head swinging briefly, BL backed off and moved away.

Pawing. Pawing was observed in both agonistic encounters and in what might be considered as ineffective "bedding"

activities preceding lying down. Pawing in aggressive encounters (Tables 17 and 18) was closely related temporally to patterns such as horning and gland-rubbing and may be related to the digging of shallow pits in the soil reported by Tener (1965).

I saw only two pits in the soil in 1968, both of which appeared to have been dug the previous summer. The only "pit"-digging behaviour I observed occurred on 20 September, 1971. An adult bull (B1) in a herd of 23, was repeatedly sniffing and following cows. As a second bull (B2) approached, B1 began rubbing against the ground. After head-tilting, gland-rubbing, rubbing and horning near B1 and the cow, B2 pawed three times with the left foreleg then rubbed his muzzle and horns in the hole pawed through the snow. Both bulls rubbed vigorously, then B1 watched as B2 head-tilted around him again. After B2's second bout of gland-rubbing, B1 turned and moved away. Again B2 dug a pit in the snow and rubbed his muzzle and preorbital area against the sides of the hole for about three minutes.

Horning. Horning was never seen isolated from the patterns previously discussed. It usually occurred in agonistic encounters between bulls (Tables 17, 18) and in situations of disturbance.

Head-tilting. Seventy-four head-tilt displays occurred

in interactions between bulls of the same herd (Table 19). Only one instance of a cow performing the head-tilt display was recorded. In all of these within-herd interactions, only the initiator of the interaction performed the display. In 42% of the 74 interactions the recipient bull assumed the head-up position and watched the displaying bull. In 23% the recipient ran or walked away quickly (i.e., showed "submissive" or "inferiority" behaviour), in 17% he butted or charged the other and in 10% appeared to ignore the displaying bull. In 6% of the interactions the displaying bull later butted or charged the recipient.

Rubbing, gland-rubbing, horning and pawing occurred along with the head-tilt in some instances and the majority of these additional behaviour patterns were performed by the displaying muskox. None of the 74 interactions resulted in clashing.

On two occasions a head-tilt display was performed by the herd's dominant bull and directed at a subordinate bull immediately after the subordinate had been sniffing or had attempted to mount a female (Figure 21).

Clashing. I observed clashing only four times during this study. Only one clash occurred between bulls of the same herd (12 July 1968). Of the others, one involved the dominant bulls of two herds which eventually joined (31 August 1971 -

Table 19. Head-tilt display encounters in which only one of the interacting pair performs the head-tilt; showing initiator, recipient, components and result of the interactions.

	LB-LB*	LB-B	LB-YB	B-B	B-YB	YB-YB	LB-C	YB-C	C-C	TOTAL INIT.	TOTAL RECIP.	TOTAL
Head-Tilt Initiator	3 -	17 1	4 -	33 -	5 -	3 -	3 -	3 -	2 -	74	-	74
Recipient:												
Ignores	-	2	-	-	-	2	1	2	-		7	7
Watches, head-up	2	9	2	11	5	-	2	-	-		31	31
Encounters With: G.R.**	- 1	5 -	- 1	14 2	1 -	2 -	2 -	3 -	1 -	28	4	32
Horn.	- -	2 -	- -	- -	- -	- -	- -	1 -	- -	3	-	3
Paw.	- -	2 -	- -	1 -	- -	- -	- -	- -	- -	3	-	3
Rub.	- -	3 -	- -	4 3	1 -	- -	1 -	- -	- -	9	3	12
Charge	- 2	1 1	1 -	- 1	- -	- -	- -	- -	- -	2	4	6
Butt	- 2	2 -	- -	1 3	- -	1 -	- -	- -	- -	4	5	9
Approach without butt	-	1	-	2	-	-	-	-	-		3	3
Encounters ending in:												
Fight	-	-	-	-	-	-	-	-	-	-	-	0
One animal departing quickly	- 2	- 2	- 4	- 6	- 1	- -	- 2	- -	- -	-	17	17

* LB = dominant bull, B = adult bull, YB = subadult bull, C = Cow

** C.R. = gland-rubbing, Horn. = Horning, Paw. = Pawing, Rub. = Rubbing

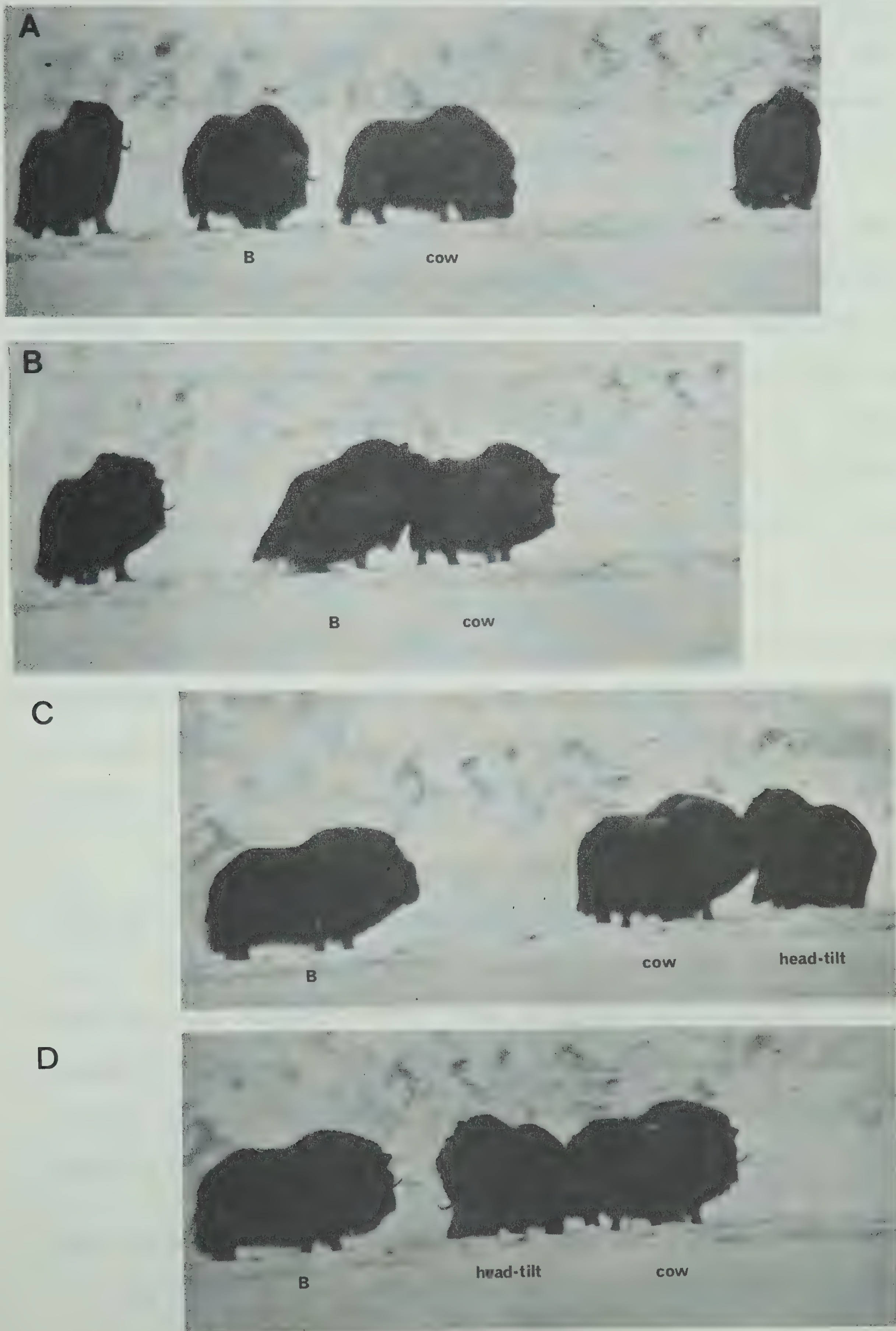
Figure 21 Head-tilt display performed by a dominant bull following an attempted mounting of a cow by a subordinate bull.

A. The herd stands facing towards the observer,

B. An adult bull rushes an adult cow, rises onto his hind legs and briefly mounts the cow,

C. The dominant bull (far right) begins a head-tilting display after the cow moves away from the other bull (left),

D. The dominant bull continues the head-tilt display and circles around in front of the watching bull.


A
B
cow
B
B
cow
C
B
cow
head-tilt
D
B
head-tilt
cow

this clash is described in detail in a later section), and two involved bulls from two herds which remained separate after the clash (2 August 1968, 21 August 1969).

In the clash between bulls from the same herd, the dominant bull of the herd appeared to "win." After three charges, he successfully pushed the other bull backwards until the other broke away and ran off. A cow which had been feeding with the dominant bull before the clash, ran behind him in the last of the three charges (Figure 20). The herd moved off together soon after the clash, with several butting interactions occurring among the bulls.

In all clashes, the head-tilt and gland-rubbing displays preceded backing up (with head-swinging) and charging. Head-to-head pushing followed the charges and sideways jabbing or hooking with the horns occurred twice.

P. Taylor (pers. comm.) observed a dominant bull chasing and repeatedly hooking another bull that was attempting to rejoin the herd after becoming aware of the observer's presence (21 August 1971). The dominant bull had originally attacked the other following his own active courtship of several cows. The hooked bull's hind legs were red with blood and he limped noticeably following the encounter.

(ii) Initiation of Interactions. Because subtle motions such as movement of the ears and eyes ("accessory co-ordinations,"

Tembrock 1963, Walther, in press) could not usually be detected due to the distance between observer and muskox, the first muskox to make an obvious movement (or "major co-ordination") which could be considered part of an interaction, was considered to be the initiator of that interaction.

In herd 69-A-4, considering displacement interactions among the bulls only, the dominant muskox was the initiator in 98.9% of 93 interactions (Table 20). In the case of butts and charges the dominant muskox initiated 53.9% of 39 interactions and 30% of 10 interactions respectively. In simple butting and charging interactions (excluding herd 69-A-4) where the dominance relationship between interactants was known, the subordinate initiated seven and won none of the interactions, and the dominant initiated two and won five.

In a 60-minute butting "session" among the four bulls of herd 68-C-4, just after the fourth bull joined the original three, 34.6% of the recorded butts (n = 26) involved a subadult bull. This subadult (and subordinate) bull initiated 11.5% of the butts and a mature bull initiated 7.7%. I could not determine the initiator in the remaining interactions.

Only 1 out of 74 one-sided head-tilt displays recorded was performed by a clearly subordinate bull. However, of the "aggressive"-type responses following the display, 17% were initiated by the recipient and only 6% by the performer.

Table 20. Interactions between the bulls LB, 2B and 1B of Herd 69-A-4 showing initiator and winner.

LB Initiated:	42	displacements	with	2B	and	won	42
	21	"	"	1B	"	"	21
	3	butts	"	2B	"	"	5
	2	"	"	1B	"	"	2
	0	charges	"	2B	"	"	2
	0	"	"	1B	"	"	0
2B Initiated:	0	displacements	with	LB	and	won	0
	29	"	"	1B	"	"	29
	1	butt	"	LB	"	"	0
	16	"	"	1B	"	"	25
	3	charges	"	LB	"	"	0
	3	"	"	1B	"	"	2
1B Initiated:	0	displacements	with	LB	and	won	0
	0	"	"	2B	"	"	1
	0	butts	"	LB	"	"	0
	17	"	"	2B	"	"	3
	0	charges	"	LB	"	"	0
	4	"	"	2B	"	"	1

(iii) Characteristics of the Dominant Bull. It is not too difficult for an observer to pick out the dominant bull in most muskox herds through the behaviour of the bull and the reactions of the other herd members. Most dominant bulls were among the largest bulls of the herd and had the large, dark-coloured, cracked horns, which may be characteristic of older animals (Tener, 1965), plus relatively large amounts of unshed wool clinging to the mane and rear "skirts."

When a dominant bull walked through a herd, subordinate bulls, especially subadults, moved quickly out of his way and stood watching with heads raised. When subordinates were displaced from very close range, they usually ran from the dominant bull with heads held high, turning from side to side to keep the dominant bull in sight. The dominant bull was often the last member of the herd to respond to an object or animal approaching from a distance and the first to "relax" when the object had passed (Figure 22). In several cases when a resting herd was disturbed by a distant object or animal, the dominant bull did not rise and group with the others.

On the other hand, when a herd was approached very closely, the dominant bull was most active in gland-rubbing and pawing and moved through the herd, butting other bulls out of his path, keeping close to the source of the disturbance.

Limited observations of an all-cow herd (69-D-10)

[illegible]

[illegible]

[illegible]

[illegible]

Figure 22 Behaviour of a herd of seven muskoxen following disturbance by a low-flying Otter aircraft, 16 June 1968.

A. Herd tightly grouped at approach of aircraft, time: 1440 C.D.T.,

B. Aircraft overhead for second and final pass, time: 1445,

C. Dominant bull, "LB," horning ground, time: 1450,

D. One adult bull feeding, dominant bull lying down, time: 1451,

E. Two adults and subadult bull feeding, dominant bull and one other lying down, time: 1454,

F. Four muskoxen feeding, three lying down, time: 1455.

A

B

C

D

E

F

showed that the dominant cow had some of the same behavioural characteristics as the dominant bull of a mixed herd. In herd 69-D-10, a large, very light-coloured cow dominated others in the few displacement-type interactions recorded, was the last to rise at the approach of humans and responded to our presence with very vigorous gland-rubbing. When the herd stampeded with one cow successfully marked, the dominant cow fell far behind the others. When they stopped running and grouped, she did not approach them but kept galloping along in a direction parallel to their course. The herd then ran towards her and followed her into the hills. When the same herd reappeared 11 days later, the same golden-coloured cow led the herd down out of the hills.

(iv) Male-Female Agonistic Interactions. Of the agonistic patterns described above, only displacements and rubbing or gland-rubbing in non-social or interspecific situations were performed by females. A few instances of unusual and irregular sequences of behaviour were the only exceptions. For example, on 25 July 1969, a cow left her herd and walked from the marshy area in which they were feeding up onto a snowbank. For the next five minutes, she performed, in the absence of a "partner," all of the patterns seen previously only in clashes between males, i.e., backing up, headswinging and charging. In addition, she gland-rubbed, leaped about tossing her head, ran up and down the snowbank and leaped backwards up the snowbank. The patterns were not performed in any sequence and

were interrupted by short periods of standing quietly. Another example of females performing agonistic patterns occurred on 27 May 1970. During an hour at midday, the members of a herd of seven (four bulls, three cows) engaged in irregular and incomplete butting, charging, clashing, or chasing encounters involving male-female pairs, three bulls and on two occasions, most of the herd.

b. Behaviour between Herds

The behaviour of individual bulls, especially the dominant bulls, during encounters between herds provided additional information relating to the function of several agonistic behaviour patterns.

The following examples of inter-herd interactions are divided into three main categories based on intensity and kind of the interactions between herd members.

(i) Two herds approach but do not join. On 1 June, herd 68-A-11 moved over a hill and down onto a flat marshy area in which a herd of 5 were feeding. The 11 moved down the slope hesitantly, bunching, then running briefly. One bull began rubbing his horns and face against a hard snow-drift, a second bull smelled then rubbed the same place, while a third bull gland-rubbed beside him. This bull gland-rubbed vigorously, then rubbed a patch of bare ground. As the herd continued down the slope, two bulls butted briefly.

In the herd of 5, one bull gland-rubbed and moved across the path of the 11 (now about 200 m distant) in a broadside display. When the herds were about 100 m apart, a bull of the five began rubbing against a snow-drifted rock. When he moved, a second bull pawed at the same place, sniffed, gland-rubbed, turned and butted a third bull standing behind him. The third bull moved up, sniffed, rubbed, and pawed at the place, gland-rubbed, then rubbed his muzzle across the rock and snow, one side then the other. The herd of 11 kept moving, parallel to the 5 (also moving). Two bulls of the 5 again butted, another rubbed against a patch of ground, the 11 ran briefly and the herds slowly separated while all animals fed.

On 8 August 1969, a herd of four bulls approached a resting, mixed herd of five. Two of the four stopped and watched the five with heads raised. One bull of the five rose and began feeding. The four continued to feed within 50 m of the five. As the others of the five rose, the four bulls looked at them briefly, then two of the four lay down. The five gradually moved away, feeding, as the four began a resting period.

(ii) An individual leaves one herd and joins another. On 27 July, a cow walked away from herd 68-D-3 towards herd 68-B-5. As she approached, three of the five stopped feeding and watched her. She then stopped, fed briefly and stood, with head up, within 20 m of the herd. The herd moved towards

her and a subadult bull gland-rubbed twice. She remained standing as a second bull gland-rubbed while the first walked in front of her, presenting his broadside. A third bull, the dominant bull, approached her, and moved up beside as she moved sideways. When she moved again, the bull followed, sniffed her rear twice, then lip-curled. He moved up and sniffed again, then moved to the side and all animals resumed feeding.

(iii) Two herds join; with little or no interaction. One herd of nine approached another resting herd of nine (both herds had five bulls and four cows) on 5 July 1969. As two bulls of the approaching herd neared the other, one bull got up and stood looking at them with head raised. As he gland-rubbed and did a head-tilt display toward the two, one of them watched, head up and the other began feeding. All fed briefly, then all three lay down. One cow of the approaching herd joined two cows of the second herd, then all animals began feeding and the herds mixed.

Two herds join; after the lead bull of one herd interacts with members of the other herd. The dominant (and only bull of herd 71-A-6 moved out to meet an approaching herd of eight bulls on 30 September during a moderate snow storm. As he moved forward, he gland-rubbed several times, then began head-tilting. The first four head-tilt displays were directed at the first six bulls of the other herd, all of which responded

by standing with heads up and watching him. He then moved back through the herd, butted with one, approached, head-tilted to, then butted with a second while two others also butted together. The fifth and sixth head-tilts were accompanied by gland-rubbing and were directed at one bull of the eight. The dominant bull rubbed on a snow-drift and turned away to head-tilt towards another bull. The recipient of the sixth head-tilt rubbed on the same snow-drift after the dominant bull had left. Two of the eight bulls butted twice while the others began feeding near the five cows which had remained lying down during the interaction. All animals then began feeding.

A herd of 11 galloped in a tight group towards a herd of 20 feeding about 1 km away on 17 October, 1970. The herd of 20 grouped and ran a short distance away, then stopped and faced the approaching herd. The dominant bull of the 20 moved forward and faced, sniffed and circled the leading individuals of the 11 before the herds mingled. I was not able to determine which was the dominant bull of the herd of 11.

Two herds join; after the dominant bulls of both herds interact. The following account of a clash between the lead bulls of herds 70-B-7 and 70-D-5 is presented here in detail because this interaction contained all of the previously described patterns of agonistic behaviour.

The interaction occurred on 31 August 1970 and lasted from 1250 to 1515 C.D.T. At 1215 the dominant bull of herd 7 (=LB) began moving towards herd 5. Four muskoxen in the other herd stood, heads up, watching the approach. The dominant bull of herd 5 (=5B) began strutting, pawing and rubbing at 1255. Another mature bull of the 5 rubbed at the same location as 5B did, and 5B, facing herd 7, gland-rubbed once. At 1300 LB began pawing and rubbing also. During the bouts of rubbing each bull shook his head vigorously once. Both horned the snow-covered ground then walked parallel to each other in a low intensity head-tilt display. At 1305 two cows from herd 5 rubbed on the same place previously rubbed by 5B and the other bull. While 5B continued rubbing, LB walked, then ran, towards herd 7. As he reached his grouped herd, the bulls stood watching him in the head-up position and the cows ran away from him. Then 5B approached LB, both walked parallel, gland-rubbed and walked back in the opposite direction, head-tilting. Two cows of herd 5 walked along close behind 5B and six of herd 7 followed about 12 m behind LB.

At 1336, 5B again began rubbing vigorously. As LB moved towards him, several cows ran out of the way. After a bout of gland-rubbing LB moved to 5B and they butted briefly. Both bulls backed up from the butt, headswinging, then charged forward in the first of 16 charges.

At impact, neither bull gave way at all. In most cases LB backed up farther and faster than 5B and his head-

swinging was more exaggerated and vigorous. The average time of backing up in 13 timed charges was 24.7 sec and the maximum distance covered was approximately 45 m. In seven of the ten charges in which I was able to record the first bull to back up, 5B began backing first, and in one both began simultaneously. In nine of the thirteen charges in which I recorded the first bull to charge forward, LB was the first. Following 30 sec of backing which covered about 45 m, one charge (from takeoff to impact) lasted about 3 sec, giving an approximate charging speed of 15 m/sec.

During the 17 min of the clashing proper, one cow from herd 5 dashed between the charging bulls, one animal from herd 7 chased another from herd 5 and the two herds gradually mingled. Some stood watching the bulls, others moved slowly away.

At 1350 the bulls began pushing head to head briefly before backing up. After the sixteenth charge, the two engaged in a pushing contest which lasted 6 min. During most of the pushing bout, 5B was successful in pushing LB backwards and LB seemed to lose his footing twice. At one point, both gave several sideways-jabbing hooks with the horns, then resumed pushing.

At the end of the bout, the bulls hesitated briefly then began circling with heads still together. Bull LB was

being pushed steadily backwards. Suddenly LB's horns slipped from 5B's and he delivered a quick hard blow to 5B's side. Immediately, 5B ran from him. As LB walked towards him, 5B turned and faced briefly, then ran again. When 5B stopped and faced him again, LB head-tilted around 5B. Two other bulls followed LB as 5B continued to walk away. At 1401, LB stopped following 5B and began rubbing and horning on a mound. His actions were vigorous and he tore off chunks of turf with his horn tips. This bout of rubbing, gland-rubbing and horning lasted 10 min.

While 5B moved back closer, a second bull from herd 5 also began rubbing on the mound beside LB. As 5B approached, the second bull ceased rubbing and walked away from LB. The mixed herd was moving away and LB started off towards them, stopped, approached 5B and the other bull (=OB) and began rubbing again. Twice, LB circled around the two, gland-rubbing and alternating between facing the herd and facing the bulls. At 1450 all three bulls fed briefly. At 1505 LB walked along the lake separating them from the herd. At 1515 5B and OB started walking in single file, with 5B leading, steadily away from LB and the herd, towards the far side of the valley.

At 1552, LB reached part of the herd and in the next 20 min, he followed, sniffed and chased several cows. By 1630, LB, the cows and the rest of the herd had moved over a hill and

[illegible]

[illegible]

[illegible]

[illegible]

out of sight. At 1945, OB and 5B were still steadily moving away, at a distance of about 10 km from the site of the interaction.

Another, much shorter clash was observed by D. Gill (pers. comm.) on 13 June 1972, in which tagged bull #71-1, accompanied by a cow, approached a herd of six (5 B's, 1 C). The dominant bull of the herd and bull 71-1 both gland-rubbed vigorously, backed up, headswinging, and charged. The marked bull knocked the other to a sitting position then backed up again. The other got up quickly, turned sideways, then walked away. Within 30 minutes, the "defeated" bull had rejoined the new herd with no further interactions occurring.

3. Interspecific Agonistic Behaviour

Many of the behaviour patterns observed in encounters within and between herds are also seen in interspecific interactions. The pattern of grouping together in a circle to face attacking wolves or man is the basic behaviour pattern with which these others are usually associated. Although this behaviour has been described often (see Hone 1934, Tener 1965) many recent accounts are distorted or poorly detailed (eg., Stonehouse, 1971).

A generalized, typical reaction of the Bathurst muskoxen to the approach of wolves or man begins with one or more individuals perceiving the object and assuming the at-

tention or alarm posture. As the object or animal approaches, one muskox, usually a female, begins to run, and the others then all run towards the dominant bull, towards high ground or to an area of shallow snow. Depending on the circumstances, the herd may continue galloping away in a tight group or will stop and stand on the high ground and turn to face the approaching stimulus. It is usually the dominant bull who first turns and stops and the others wheel around behind him. Initially, a line abreast formation is formed with the musk-oxen all pushing together sideways and, in larger herds, those in back crowding through to the front or pushing around to the ends of the line. Often the dominant bull will remain out in front of the line. If the wolves or humans circle the herd, the muskox in line will form a rough, solid circle or rosette by pushing their rear ends together. This pushing of rear ends together is seen in pairs as well as in large herds and is the same behaviour as that shown by solitary bulls as they back up to a boulder or bank when pressed by an attacker.

Most animals in the herd, both cows, bulls and sub-adult animals, perform the gland-rubbing behaviour when the "danger" approaches to within 50 m. The lead bull usually gland-rubs more vigorously and may also horn and rub against the ground. If the herd is pressed closely (by man) much pushing, butting and snorting will occur. Individual cows or bulls will charge a wolf or man that has approached too

closely, then will return to the herd.

In the following section, observations of interactions between muskoxen and some other species are presented. Wolves and man are the only natural predators of muskoxen; however, the behaviour shown by muskoxen in encounters with other species (arctic fox, polar bear, caribou and arctic hare) contains the same basic components.

a. Muskoxen and Arctic Wolf

I have previously described, in some detail, the behaviour of a solitary bull muskox when attacked by a single wolf (Gray 1970b). Several other observations of wolf-muskox encounters are described briefly here. These and other observations will be presented in more detail elsewhere.

On 16 September 1970, six wolves (four adults and two young) approached herd 70-F-10. The muskoxen moved closer together but did not form a tight defensive group. The wolves stood watching the muskoxen briefly, then moved away. Later that day the pack attacked herd 70-E-12. Only the four adults took part in the attack in which the wolves circled the herd, leaped up at and attempted to cut off individual bulls and cows that charged out at them. The herd seemed disorganized until the dominant bull charged and vigorously butted two muskoxen as they began to run from the grouped herd. Afterwards, each time a muskox charged a wolf, the whole herd

moved together behind the charging animal, closing the gap and preventing the wolves from cutting in between. Both muskoxen and wolves rested for 2 hours after 25 min of action. The wolves renewed the attack for a further 10 min, then departed.

On 4 March 1971, a male-female pair of wolves attacked a herd of 23 and succeeded in killing a pregnant cow after she dropped back from the stampeding herd. The cow held off the wolves for at least 50 min. Unfortunately, a bank of fog obscured the area and the end of the fight was not seen. The wolves remained in the vicinity of the carcass for at least 2 days.

The same wolf pair killed a second cow on 24 March. The initial attack was not seen but again the herd stampeded, leaving the cow and wolves at the place where the herd had been feeding. The cow fought the wolves for 30 min by charging and attempting to hook with her horns. Then both wolves moved away and lay down for 40 min. The attack was renewed and lasted for at least another hour before darkness obscured the action. The horns of this cow were curved in towards the orbits and would have been very ineffective as weapons. The length of time it took the two wolves to bring down this cow is interesting when compared with the 53 min it took a single wolf (very likely the same male) to bring down a subadult bull in May 1968 (Gray, 1970b).

b. Muskoxen and Arctic Fox

Muskoxen only reacted to foxes passing within less than 100 m. They responded by raising the head to the attention posture and, in some instances, by gland-rubbing. On 5 June 1969, a fox approached to within 3 m of herd 69-A-4 and began play-stalking the herd in a typical canid manner, leaping back and forth with lowered forelegs and tail waving side to side. Two of the muskoxen, 2B and C, raised their heads, then 2B moved to C and pushed his rear against hers. The bull 1B, who hadn't noticed the fox, suddenly wheeled around, watched the fox briefly, gland-rubbed once, then resumed feeding as the fox continued to crouch and circle in front of the herd.

c. Muskoxen and the Polar Bear

Bears were seen in the study area about once a month during summer, but were seen near muskox herds on only two occasions. On 31 July 1968, a bear passed downwind and within about 200 m of a feeding herd of three muskoxen, and no reaction was observed. However, on 4 July 1969, when a bear walked past within 100 m of herd 69-C-11, the herd ran a short distance, grouped briefly, ran again for another 50 m, and then regrouped. The muskoxen remained wary for the next 30 min and stood looking around, with heads raised, long after the bear had disappeared from view.

d. Muskoxen and Caribou

Although muskoxen and caribou graze in the study area, they tend to utilize different parts of the habitat. Both species were often seen grazing within 100 m or less with neither paying any noticeable attention to the other. The caribou were constantly on the move and did not remain in an area for more than a few minutes, in contrast to the muskox herds which used an area for several days. Therefore the opportunities for direct interaction were few.

Muskoxen usually watched an approaching herd of caribou with raised heads, but more complex "interactions" do occur. On 23 June 1968, a bull caribou approached herd 68-A-7 and slowly walked to within 150 m. The herd ran for about 50 m, then grouped in a rough circle with the dominant bull, CB, in front. One bull and one cow each gland-rubbed once, two other bulls moved forward and as the caribou walked by 30 m away, they all swung into a straight line-abreast formation facing the caribou. The subadult bull, YB and the cow, WC, slowly rubbed their rears together as the caribou trotted away.

A herd of 18 caribou approached a herd of 4 adult bulls on 14 September 1971. As the caribou moved straight toward the bulls, all 4 stopped feeding and watched the caribou. The caribou, strung out in a line, moved to within

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30 m of the muskoxen and each individual looked at the bulls as he passed. One bull gland-rubbed several times as the caribou moved by.

e. <u>Muskoxen and Arctic Hare</u>

On the few occasions when muskoxen and hares were seen feeding in close proximity, the muskoxen ignored the hares or watched them briefly with heads up. One exception to this occurred on 25 June 1968, when two hares ran through herd 68-A-7 passing within 10 m of the feeding muskoxen. The subadult bull, YB, gland-rubbed once as the first hare passed him and an adult bull and cow WC both watched with heads raised. When the second hare ran past YB, he just watched it and the others ignored it as it ran through the herd.

4. Discussion - Agonistic Behaviour

Tener (1960, 1965) stated that "a social hierarchy has been found in herds studied intensively and continuously." However, neither he nor Harington (1961), who also mentioned the existence of a social hierarchy, indicated which studies they were referring to nor did they present any data to demonstrate the existence of a social hierarchy other than examples of dominance of one age group over a younger age group.

The data presented here indicate, among the bulls of a herd, the existence of a linear dominance hierarchy similar to that reported for bison by McHugh (1958) and Egerton (1962).

Because of the difficulty in recognizing individual cows, I have not been able to determine whether a linear dominance hierarchy also exists among the cows of a mixed herd. Bellaar-Spruyt (pers. comm.) has reported that such a hierarchy does exist in herds at the muskox domestication project in Fort Chimo, Quebec.

The agonistic interactions between bulls fall into three main groups; the displacements, butting and charging, and the more expressive behaviours i.e., gland-rubbing and head-tilting.

A move by one muskox to displace another was seldom

[illegible]

challenged, suggesting that the displacing animal "knows" his own position relative to the dominance of the other. The fact that the muskox displaced usually moved out of the way before contact was made also indicates an awareness of his dominance, relative to that of the approaching muskox. Displacements seem to occur between animals between which an established dominance relationship existed.

In contrast to the established order seen in displacements, the movements of butting and charging were far less ordered or consistent. Butting and charging interactions were often initiated by subordinate bulls. These behaviours seem to function as a test of strength, a means whereby a younger or subordinate bull can become aware of his strength and "practice" or test components of the clash against a dominant with little probability of injury or involvement in a serious fight. The pushing in the head-to-head position which often followed a butt or charge also suggests a testing of strength between individuals.

Butting, under conditions of disturbance, has been described as a "displacement activity" resulting from a conflict between attack and escape drives (Tener 1965, Bos 1967). Since most instances of butting occurred while the muskoxen were already in flight, any such conflict must already have been resolved and thus explanation in terms of the displacement activity theory must be discarded. Another objection to the displacement activity hypothesis is that irrelevance is

one of the main characteristics of such activities. Butting or charging in an agonistic situation cannot really be considered irrelevant.

This kind of behaviour might be more logically described as redirected aggression. But that explanation might also be complicating the problem unnecessarily. The level of aggressive motivation is probably high in these situations but the aggression is not redirected unless an appropriate stimulus to "trigger" the aggressive pattern is provided. The fact that a running muskox bull is treated as an offensive threat in many circumstances suggests that butting in a running or a stampeding herd may simply be a response to this threat. On many occasions, bulls were seen to wheel around and face another bull approaching quickly from the rear. The approaching animal, in turn, may see the facing bull (with its head in a position to receive or deliver a butt) as a threat directed at him and thus continue on to complete the run as a charge, or veer to the side or halt abruptly. If butting or charging is simply responding to the stimulus of a head position of another bull or a running animal, then there is no need to invoke redirection as an explanation.

Interpretations of the function of the gland-rubbing behaviour include such ideas as sharpening of the horns by rubbing them against the foreleg (Hall, 1879, in Hone 1934) and Pedersen's (1958) suggestion that the secretion produced

by rubbing lubricated and matted the hair of the brow and kept it out of the eyes during a fight.

Tener (1965) rejected Pedersen's suggestion, pointing out that any such matting is at best ineffective and that the secretion couldn't function this way at freezing temperatures in winter. However, we do not know the freezing point of the secretion. In any case this explanation can be discarded since the hair of the brow could only cover the eyes in summer when the wool is being shed.

Pedersen also noted that the amount of secretion was greater after a long test or disturbance and that the secretion seemed stronger during the rut. He suggested that the gland might serve a reproductive function during the rut through production of scent.

Tarasov (1960) stated that scent-marking in muskoxen served to mark territorial boundaries. This statement seems to be based on the presence of the glands only, and not on original field observations. Since muskoxen are considered to be non-territorial animals, Tener's (1960, 1965) criticism of Tarasov's interpretation is valid.

It seems quite reasonable to assume that muskoxen rub the preorbital gland on the foreleg in the absence of suitable rubbing "posts" in the environment (Harington, 1961). Muskoxen on the Canadian mainland spend much time in the willow

thickets along river banks and are known to thrash the bushes with their heads (Kelsall, 1951). Hanbury (1904, in Hone 1934) described the "horning" of trees by muskoxen in the Thelon River area. Similarly, I have observed muskoxen rubbing the gland on hummocks, snow-drifts and the ground (Table 10).

Ewer (1968) has suggested "self-reassurance" as a possible function of scent-marking in agonistic encounters in certain species. In order to use this term correctly, one would first have to demonstrate by definition, that the animals have lost confidence and second, that this confidence has been renewed. In most studies of scent-marking (eg., Ralls 1971, Walther in press), it has been shown that scent-marking is usually the prerogative of the dominant animal. "Self-reassurance" would seem to be necessary only for subordinate animals. Perhaps the meaning Ewer intended was self-assurance rather than self-<u>re</u>assurance.

If, as Ewer suggested, scent-marking is self-reassuring, this might lead to the biologically undesirable situation where a subordinate animal, facing a dominant, would not retreat or show submissive behaviour but instead might engage the dominant in an aggressive interaction as a result of scent-marking increasing the aggressive motivation of the "marker" (Ewer, 1968, p. 117). The subordinate animal would thus be more likely to become involved in a fight with an animal already recognized

as a dominant (hence, the decreasing confidence) and potentially the winner. I feel that use of self-reassurance to explain scent-marking is not at all useful or logical as presented. Self-assurance however may be a reasonable explanation for scent-marking in some of the species mentioned by Ewer (1968).

It is unlikely that scent-marking in muskoxen is self-assuring since subordinate animals rarely gland-rub or rub during an interaction with a dominant, and since muskoxen seldom sniff at the location they previously rubbed.

It is probably also wise to avoid Ralls' (1971) term "intolerance" in explaining scent-marking. In her discussion, intolerance is not defined and she does not indicate clearly why the term was chosen. Intolerance is, by standard definitions, an unwillingness or lack of ability or capacity to endure something (after the Oxford English Dictionary, 1961). The presence of intolerance can only be inferred on the basis of observed aggressive or threatening behaviour. It would seem to be less anthropomorphic and more prudent to retain an explanation based on these behaviours since intolerance can exist without the external evidence for it.

Ralls mentions the "threat" aspect of scent-marking in some species but does not develop this aspect to any extent. Ewer (1968, p. 154) defined threat as "a signal de-

noting that, contingent upon some act or failure to act on the part of the recipient of the signal, hostile action will be taken." Threat behaviour often draws attention to the threatener's size, strength, or weapons (Ewer, 1968). My data on scent-marking in muskoxen support Ralls' (1971) statement that animals scent-mark when they are dominant to other members of the same species, when they are likely to attack and when they are likely to win if they do attack. However, it seems to me that it is in these very situations that an animal is most likely to perform a threat display.

My suggestion that gland-rubbing in muskoxen functions as an inter- and intraspecific threat display is supported by a close look at the vigorous gland-rubbing performed by the dominant bull of a disturbed herd or by two contesting dominant bulls. Stretching out the foreleg is, in effect, taking a step forward, the head is lowered abruptly - in itself a threat for a clashing animal - and the hooking motion of the head and horns is repeated almost rythmically as the gland is rubbed. The abrupt change in colour pattern as the dark head moves in front of the white legs also emphasizes this hooking motion.

The function of pawing in agonistic encounters is not clear. Tener (1965) reported the digging of shallow pits in the soil but did not observe the actual digging nor the behaviour patterns preceding or following it. Pedersen (1958)

reported one observation of a bull digging a pit by scraping and beating with his forelegs. This bull urinated in the pit but unfortunately the circumstances in which this occurred are not given. Tener (1965) suggested pawing and the digging of pits functioned in a similar way to the pit-digging behaviour of mountain goats. Geist (1964) indicated that the pawing of "rutting pits" in mountain goats was associated mainly with aggression but could also appear in courtship or spontaneously.

My own observations indicate a primary relationship between pawing and agonistic encounters in muskoxen and, presumably, under "normal" breeding conditions, pawing would be secondarily related to and influenced by the rutting season.

Pawing is often used simultaneously with the gland-rubbing threat display and may share the "threat" function. Walther (in press) suggested that pawing might be a symbolic or redirected aggression derived from beating with the fore-legs during a fight. Although stamping with the hind legs is commonly seen before a muskox lies down, I have never seen foreleg stamping or beating in agonistic encounters. Pedersen (1958) does recount one observation of a bull striking the ground with the forelegs while facing human predators.

Horning is another of the expressive behaviour pat-

terns not fully understood in many of the species for which it has been described. A suggestion by Pedersen (1958) that muskoxen rub the horns against the ground to make their surfaces rough can only be attributed to a lack of familiarity with the horn structure and the behaviour pattern.

In my observations, horning was always associated with rubbing and gland-rubbing and might be considered a component of high intensity scent-marking displays. As well as threat, it also suggests redirected aggression in both inter- and intraspecific encounters.

The head-tilt display of the muskox fits well into the category of displays variously termed superiority displays, dominance displays or "Imponierverhalten" (Walther, in press), intimidation displays (Schaller, in press) or bravado displays (Geist 1971). Erection of the mane, stiff movement of the legs, broadside presentation, circling, head position, and the accompanying scent-marking behaviour are features of this type of display seen in several other species. The head-tilt display has a strong threat component in that the horns are presented towards the opponent through the sideways inclination of the head. This inclination itself may be due to looking away - i.e., "ignoring" or "refusing to notice" the opponent (Geist 1971).

In intra-herd interactions the display was almost always performed by a dominant animal and in most cases re-

sulted in submissive or watchful behaviour by the recipient.

A challenging or intimidating aspect of the head-tilt display was also evident in inter-herd interactions. When the display was performed by the dominant bull of one herd, the response of bulls in the other herd varied from adopting the watchful, perhaps submissive, head-up position (most frequent) to counter-displaying with the same pattern (rare). This display may serve as a means of allowing two strangers to establish their relative dominance positions without necessarily becoming involved in a clash.

Pedersen (1958, p. 35) described and photographed a bull head-tilting ("macht einen Buckel") to an attacking sled-dog. If Pedersen's observation was accurate and the bull was not actually displaying to another bull in the herd, it would seem that this display can also be used in interspecific encounters. I have, however, not seen it in many observations of similar circumstances.

Clashing has often been described in the literature (see Hone 1934 and Tener 1965) but these previous descriptions are sometimes inaccurate and usually incomplete. Tener (1965) was the first to describe head-swinging in subordinate bulls fighting with the dominant bull of a herd. Bos (1967) reported head-swinging by both bulls involved in a clash and interpreted head-swinging as displaying of the horns. This interpretation

seems reasonable and is supported by the observation that the position of the head at the end of each swing is similar to the position of the head in the head-tilt display.

The agonistic behaviour patterns seen in inter-specific encounters are basically the same as those seen in intra-specific interactions. Gland-rubbing, rubbing, pawing and horning for example are all used in encounters with wolves and humans. These observations are similar to those which led to Walther's (1969) tentative suggestion that Thomson's gazelles (*Gazella thomsoni*) react to predators in much the same way as they react to conspecifics.

B. Reproductive Behaviour

1. The Rut. The "rut" of a species is understood to be the periodically recurring sexual arousal of members of that species. It is usually inferred that copulation with insemination accompanies this sexual arousal (Struhsaker, 1967). During the expected rutting season for muskoxen, I saw no "complete" mountings or copulation.

Most reproductive or courtship behaviour occurred in late August 1969, 1970, 1971 and September 1970, 1971 (Table 21). Tener (1965) reported that height of the rut was during the first half of August, somewhat earlier than the data from my study area indicate. Due to the lack of information for September and October 1968 and 1969, and for August 1971, it

Table 21. Number of observations of each component of male-female (reproductive) interactions per month of the study - May 1968 to October 1971

Month -	April		May				June		July		August			Sept.		October		
Year -	70*	71	68*	69	70	71	68	69	68	69	68*	69	70*	70	71	70	71	Total
Bull:																		
Follows	-	-	-	-	-	-	1	-	6	1	1	9	17	19	16	1	1	72
Alongside	-	-	1	1	1	1	-	-	1	-	-	11	8	8	9	1	-	42
Sniffs	2	-	4	9	7	2	2	3	6	2	5	49	14	24	22	5	3	159
Noses Rear	-	-	-	1	-	-	-	-	1	-	-	6	1	4	2	-	1	16
Noses Head	-	-	3	2	-	2	-	-	1	1	-	3	3	4	-	2	-	21
Lipcurls	-	-	-	3	1	-	-	-	-	-	1	11	1	7	-	-	-	24
Head-up	1	-	-	2	-	1	-	-	2	1	-	8	2	11	3	-	2	33
Head-over	-	-	-	3	1	-	-	-	-	-	1	11	1	7	-	-	-	24
Head-twist	-	-	-	-	-	1	-	-	-	-	-	1	1	3	3	-	-	9
Kick	1	-	-	-	-	-	-	-	-	-	-	7	2	4	2	1	1	18
Rush	-	-	-	-	-	-	-	-	-	-	-	6	1	5	1	3	1	17
On Hind Legs	-	-	-	-	1	-	-	-	-	-	-	3	1	5	3	3	-	16
Mount	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	3
At Bull's Approach, Cow:																		
Stands	1	-	2	2	-	1	-	-	3	-	2	8	10	9	4	-	1	43
Moves	-	-	-	1	-	1	-	-	-	-	-	36	20	28	18	6	1	111

* Observations during two weeks only.

is difficult to make valid comparisons of timing of the rut with other reported observations.

2. Description of Behaviour Patterns

The following behaviour patterns related to sexual activity were observed during this study, mainly during the August-October period but also, to a lesser extent, at other times of the year.

Approach. There are three main circumstances where a bull muskox makes a direct walking approach towards another individual - to displace one from a feeding crater, to head butt with another bull, and to investigate a cow. Usually this latter approach occurred as a cow was moving or feeding. Often the approach was not noticed by the observer until the bull started to sniff the cow (Figure 23a).

Sniff. When a bull reached a cow, he lifted his muzzle to the anogenital region and held it there for several seconds. This pattern was the most common of the behaviours seen (159 observations) and occurred in 83% of the 135 male-female interactions. It was performed up to 10 times during a single interaction.

Lip Curl (Flehmen). After sniffing a cow, a bull sometimes raised his head so that the top of his face was horizontal and opened his mouth, curling back the upper lip

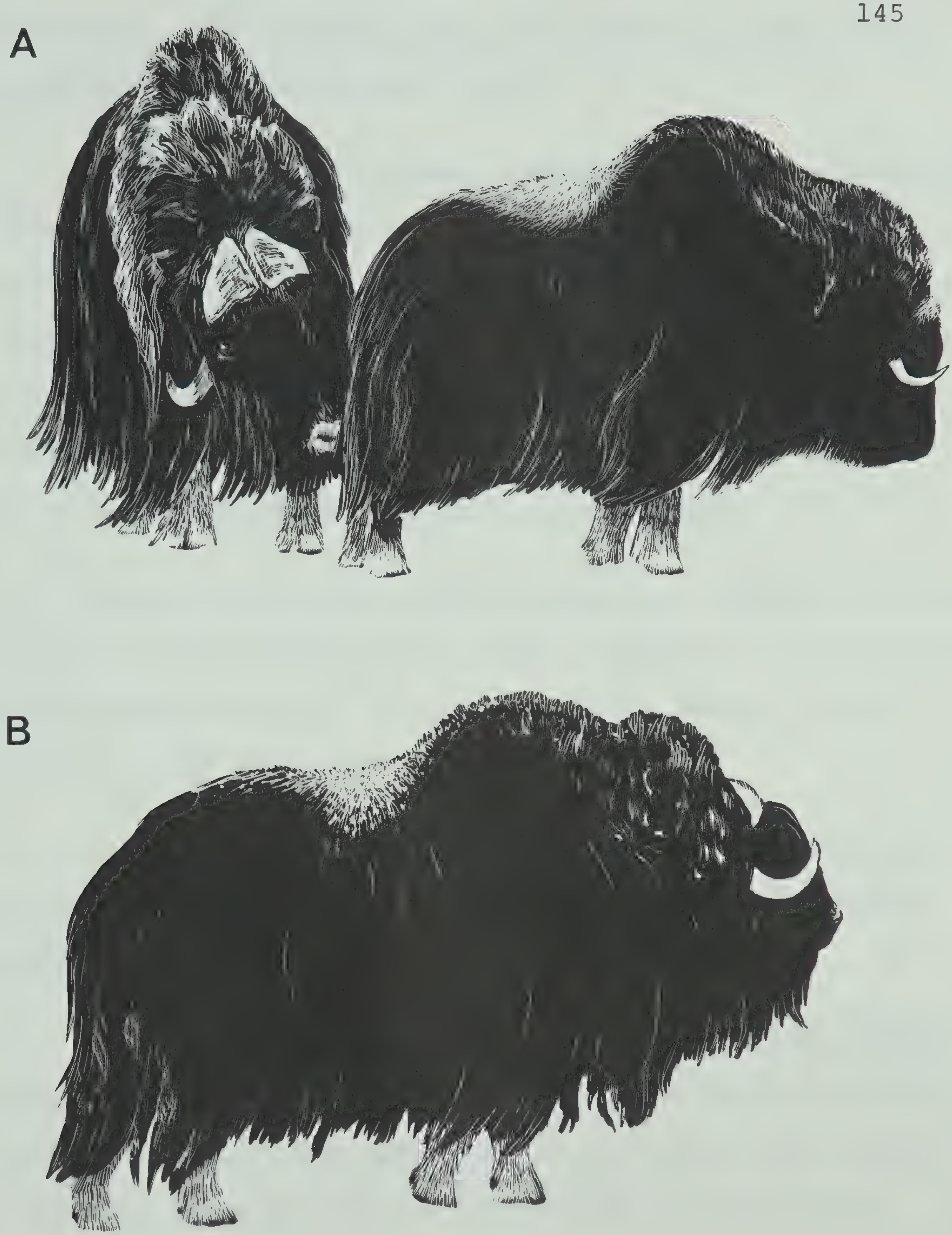


Figure 23 Adult bull muskox investigating anogenital region of cow at start of sniffing pattern (A), and lip curling after sniffing cow (B).

(Figure 23b). The pattern shown was similar to that shown by many ungulates (Schneider, 1930).

Head-up. In many cases, because of distance or light conditions it was difficult to be sure that a lip curl had occurred. When there was any doubt the pattern was recorded as "head-up." At close range this pattern was observed as a separate, distinct, pattern usually following sniffing or a lip curl. The head was held in a similar position but the mouth was not opened nor was the lip curled back.

Nosing (muzzling). Nosing sometimes replaced sniffing at the end of an approach or following sequence. The nose was pushed against the cow - at the anogenital region, in the flank, or at the head/neck region.

Head over rump. A bull on some occasions lifted his head and rested his chin on the cow's rump or back. Bulls performed this pattern from behind or beside a cow.

Foreleg Kick (Laufschlag). The foreleg kick, common to many bovids, was seen only 17 times. The kick was usually directed at the cow from behind or at the flank from beside. It varied in intensity from a gentle lifting motion to a quite vigorous kick.

Head Twist. After an approach, a bull moved up alongside the cow, then lowered and rotated his head, turning the

muzzle up towards her side or neck. This pattern was seen only nine times.

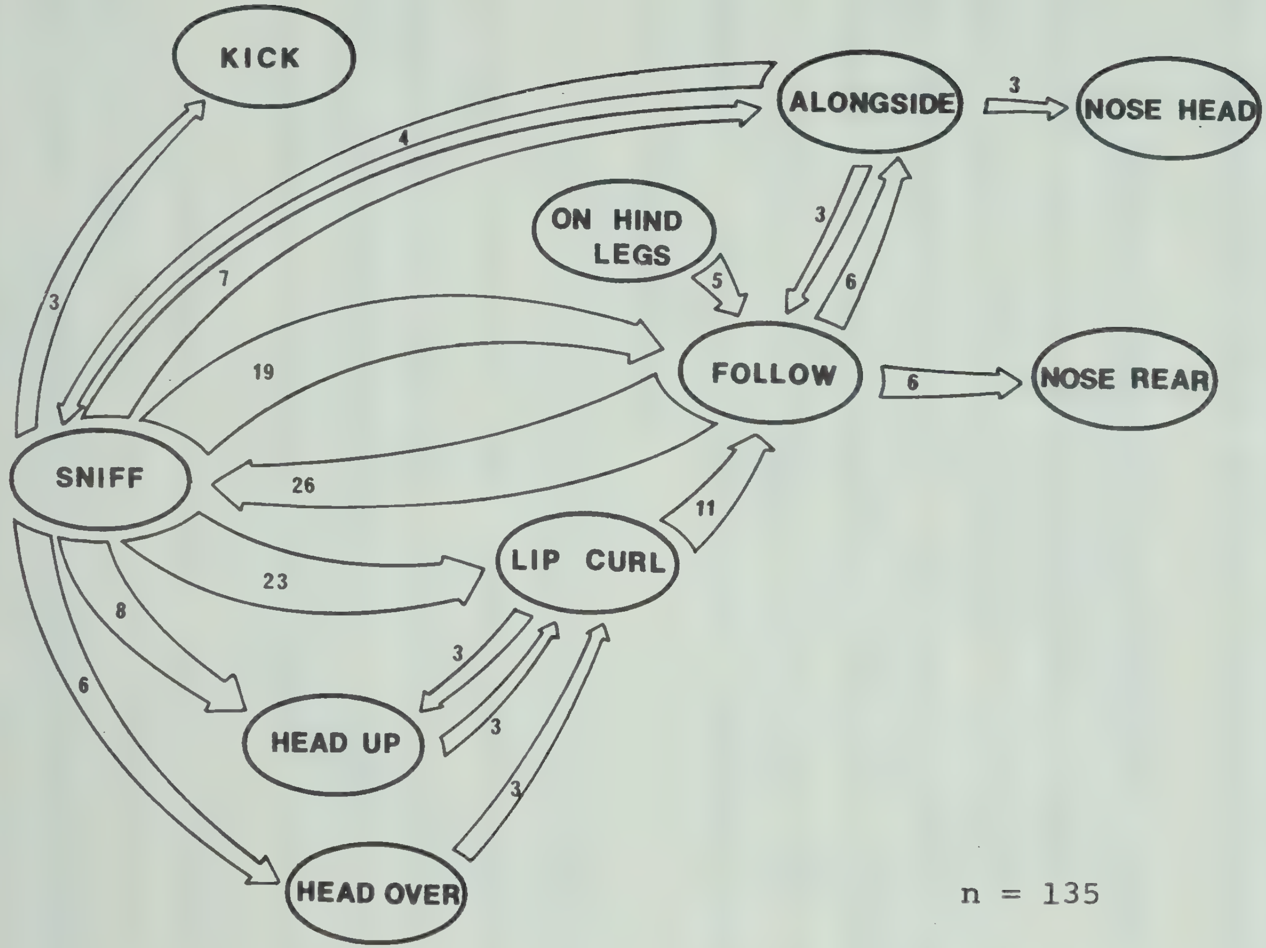
Rush. The rush is a sudden movement of a bull from directly behind the cow. If the cow did not move the bull rose up on the hind legs which in turn (if the cow still did not move) led to the mount.

Mount. Mounting was only observed three times in undisturbed herds. In all cases the mount was incomplete and lasted only one second (approximately). Several other mountings were observed during a wolf attack and one other while the herd was disturbed by the approach of an observer (see Figure 21).

Vocalizations. Bellowing or roaring of rutting bulls has been described by many authors (see Hone, 1934, Tener, 1965). I heard roaring only once (in late August) when a bull and cow were moving together from one part of a herd, that had split, to another. The roaring was repeated frequently for 20 minutes and sounded similar to the roar of a caged African lion.

3. Rutting Behaviour

The most often observed sequences for the reproductive behaviour patterns are illustrated in Figure 24. Since the initial approach of the bull is not usually distinguish-



n = 135

Figure 24 The most frequently observed sequences of male behaviour patterns in courtship interactions.

able from other movements, I have not included it in the diagram. The "sniff" is used as the starting point for the sequences. The frequency of occurrence of all sequences in the 135 courtship interactions indicates that although certain sequences are more common (eg. sniff-lip curl-follow), almost any pattern can follow any other pattern (Figure 25).

Very few sequences were observed in April, June and July and none in the period November to March. In May, however, several different sequences did occur but they were not as complete as those in the period August to September (Figure 26). The few sequences observed in October included those patterns that probably precede mounting, while those observed in the period May to July included mainly the initial investigation patterns.

Few interactions included all thirteen behaviour patterns (Figure 27). The average number of patterns per interaction (including all observations) was 4.6. The most frequently observed patterns were sniffing (159), following (72), moving up alongside (42), and lip curling (36).

A cow seldom stood still after the initial approach and investigation by a bull. Of 17 instances of a cow standing, seven occurred after she was followed by the bull whose previous sniffing resulted in her initially moving away (Table 21). Only four times did a cow stand after being touched by a bull (twice following kicks and twice following

[illegible]

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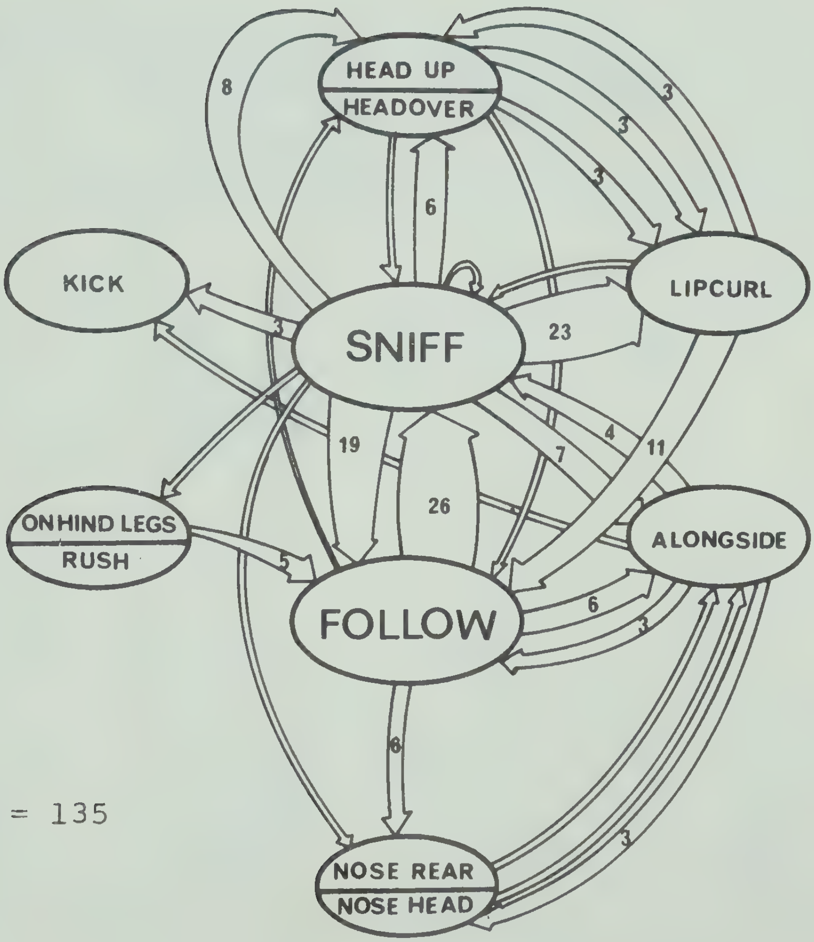
[illegible]

[illegible]

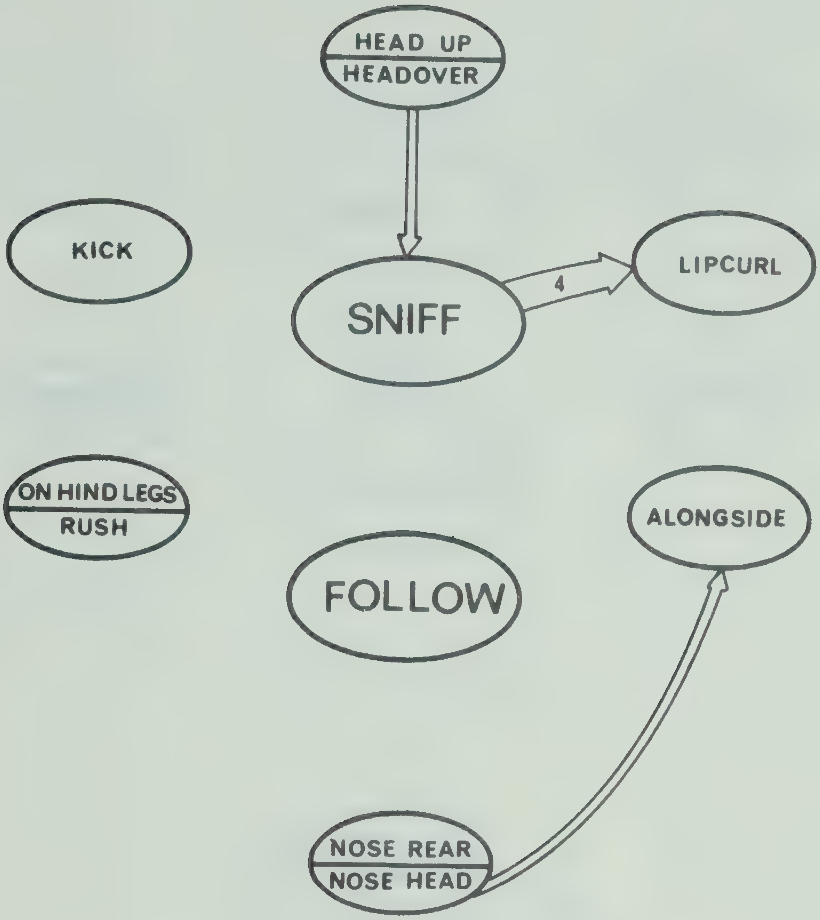


n = 135

Figure 25 All sequences of male behaviour patterns observed more than once in courtship interactions.

Figure 26 The sequences of male behaviour patterns in courtship interactions seen in each month of the study in the period April to October.

- Sequences illustrated are from the same 135 courtship interactions as Figures 24 and 25.
- Arrow width corresponds to relative number of observations of a sequence.
- Arrows without numbers indicate 2 observations.
- The "*" indicates a two week observation period only.



APRIL

Interactions:

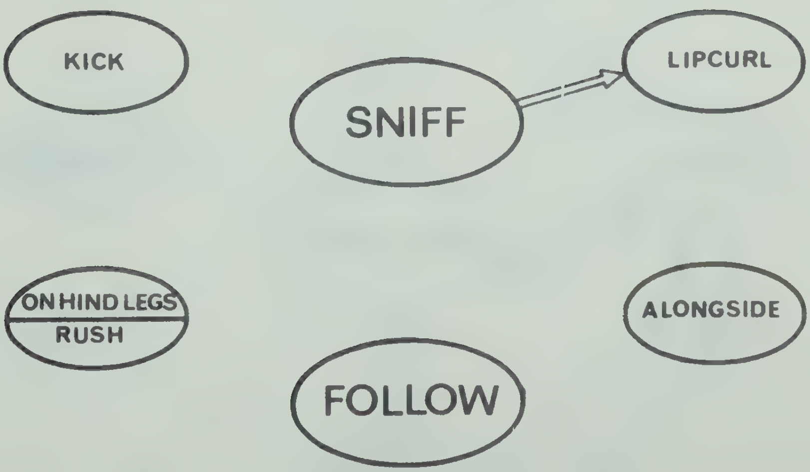
*1970 - 1
1971 - 0

MAY

Interactions:

*1968 - 5
1969 - 8
1970 - 6
1971 - 1

TOTAL - 21

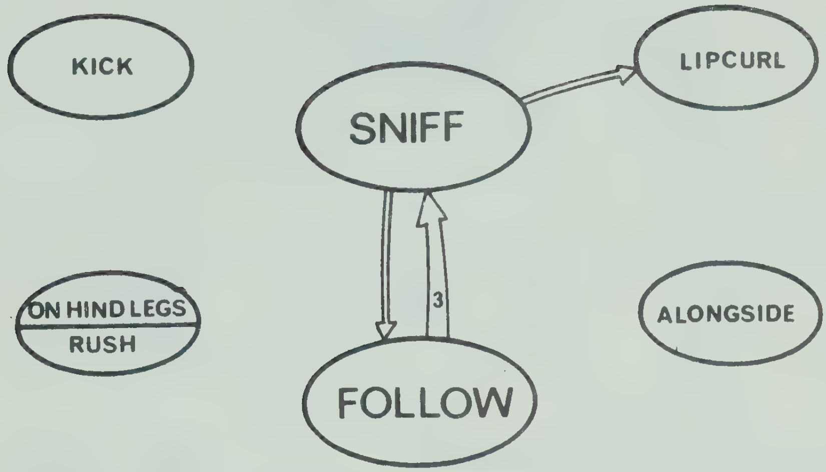


JUNE

Interactions:

1968 - 2
1969 - 3

TOTAL - 5

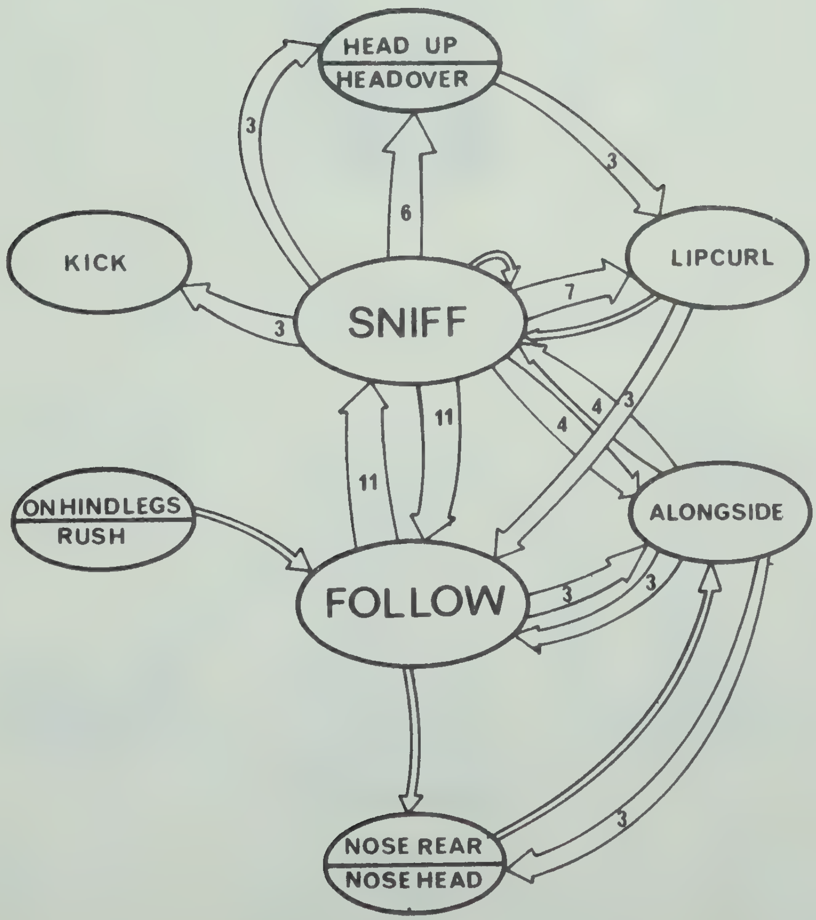


JULY

Interactions:

1968 - 4
1969 - 2

TOTAL - 6



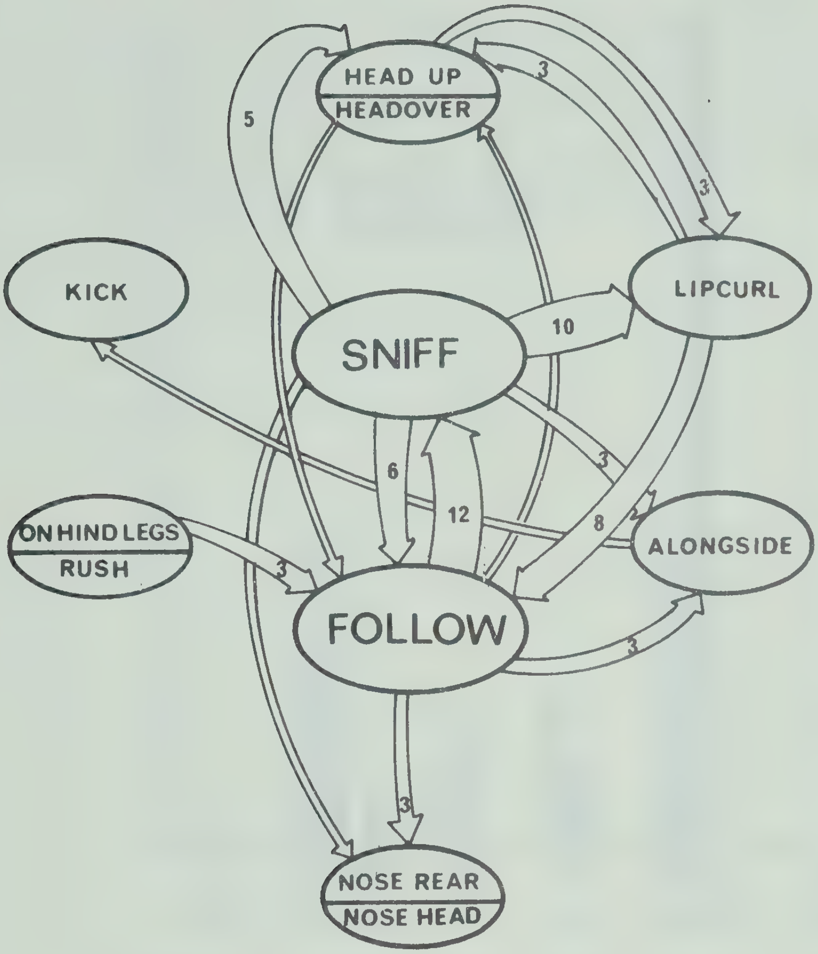
AUGUST

Interactions:

*1968 - 7
1969 -45
*1970 - 5

TOTAL - 57

Figure 26 (cont.)

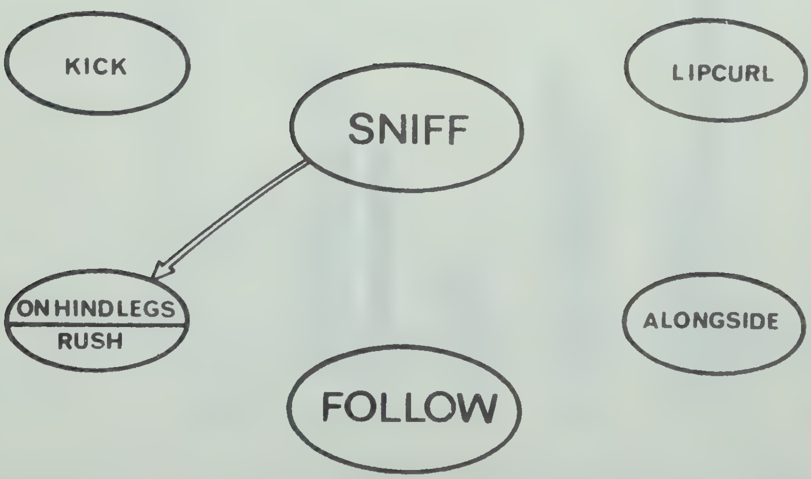


SEPTEMBER

Interactions:

1970 - 17
1971 - 19

TOTAL - 36



OCTOBER

Interactions:

1970 - 7
1971 - 3

TOTAL - 10

Figure 26 (cont.)

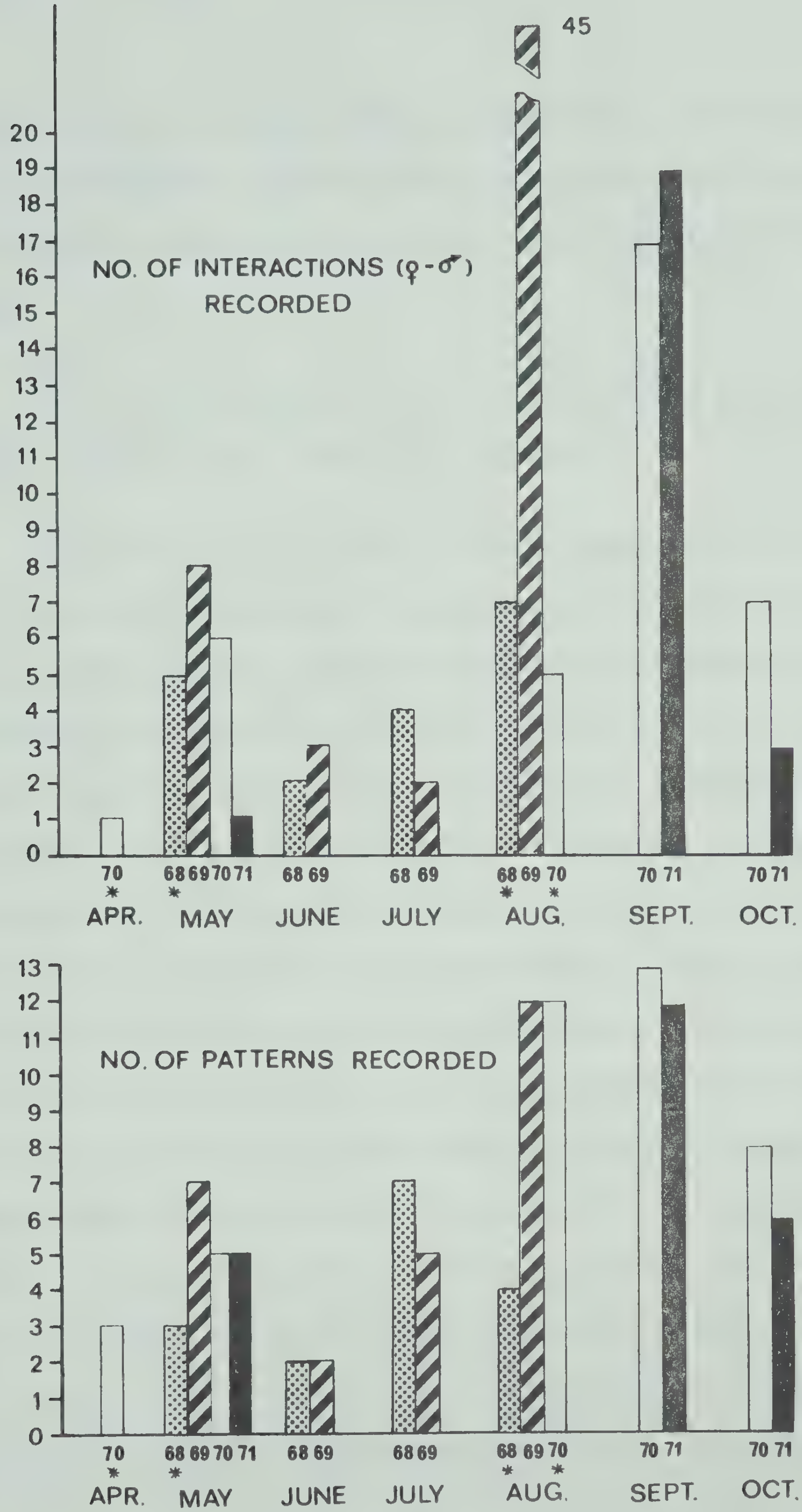


Figure 27 The number of courtship interactions and number of components (out of 13 male behaviour patterns) seen for each month of the study, April to October, 1968 to 1971. (* indicates 2 weeks observation only.)

nosing). In 10 of these cases of standing, the bulls response was another sniffing bout, in 2 the bull simply stood still and in 1 case each the bull nosed, kicked or rushed the cow.

Cows sometimes avoided courting bulls by running and no active courting by cows was observed.

On five days in August 1969, three bulls accounted for 62.2% of 45 courtship interactions recorded in that month. Each of these three bulls was the dominant bull of a different herd and two of them were, for several days, the only bull in their respective herds. However, none of these herds were considered "harems" because no evidence of the exclusion of other bulls was seen, rather the herds were formed by the splitting of larger herds. One bull was believed to be "LB," originally the dominant bull of herd 69-A-4. The most active bull, in the herd of 11 (4 bulls, 7 cows), was watched for three days, 21 to 23 August and he accounted for 36% of the interactions for the month. Although I cannot be absolutely certain that I was watching the same bull, since there was some mixing of herds, I feel confident that it was the same animal because only the one bull was active in courtship and behaved like a dominant bull.

These three bulls were involved in only 27 of 49 sniffing interactions for the month of August, but in 5 of

6 lip curls, 9 of 11 "head-over-rump," 7 of 7 foreleg kicks, 5 of 6 rushes and 2 of 3 cases of rising up on the hind legs before mounting. Thus these three bulls accounted for just over half of the initial investigatory patterns recorded, but accounted for the majority of those patterns occurring closer to mounting in the probable courtship sequence.

4. Discussion - Reproductive Behaviour

Little information is available on behaviour of wild muskoxen during the rut. Several authors described bulls "fighting for possession of cows" (Hone, 1934) and indicated that mating occurred but did not describe the actual event. Tener (1960, 1965) described "unsuccessful mating" which consisted of repeated mounting attempts but did not describe the few instances of mating that he observed. Teal (1959) and Wilkinson (1971) described only briefly courtship and mating of captive muskoxen. Both mentioned sniffing, curling of the lip, scraping or feeling the flanks of the cow with a foreleg, and mounting.

Unlike the situation reported for bison by McHugh (1958) where bulls and cows perform the lip curl following the sniffing of many odours including male or female urine on the ground, new calves, and blood, muskoxen were seen to lip curl in response to fresh female urine on the ground only twice. In all other instances, lip curls followed sniffing of a female by a bull.

Although curling of the lip in the Flehmen response is usually taken to be an indication of olfactory testing of the female's urine, Dagg and Taub (1970) reported that such testing can occur without the actual curling back of the lip. The pattern I have termed the "Head-up" in courting bulls may be a behaviour pattern which functions in the same way as the lip curl.

The bull's courtship patterns of moving up alongside, nosing the neck or flank of the cow, the gentle foreleg kick and resting of his head on the cow's rump all probably help in preparing the cow to accept mounting. At the male's initial approach his intentions might not be clear—it may be an aggressive or a courtship-type approach. The gradual increase in body contact probably helps to prevent the cow from moving away.

There is some similarity between nosing by the bull muskox in courtship and typical bovid calf-cow contacts (Hafez 1969). This similarity may also increase the likelihood that the cow will not move away. Geist (1971a) reported juvenile-like behaviour in courting mountain sheep rams.

The foreleg kick in its more vigorous form likely serves as a final test of receptivity before mounting. Walther (1958) suggested that the Laufschlag movements are derived from primitive ungulate agonistic behaviour. Because many ungulates do not use the forelegs in fighting, Lent (1969)

suggested that perhaps the foreleg kick is merely the stereotyped or ritualized start of the mounting sequence. However, for muskoxen, Walther's interpretation seems more reasonable since the foreleg kick was seldom closely associated in time with the rush, rising onto the hind legs, or mounting. The kick does appear to be part of a sequence of behaviour leading to mounting, but the basic body positions when mounting and when kicking are very different.

The head-twist is the closest thing to a courtship display in muskoxen. In some respects it is the antithesis of the agonistic head-tilt display. The muzzle is rotated towards the female and the bull performs the head-twist from an angle or parallel orientation in contrast to the broadside approach of the head-tilt. The head-twist was performed on two occasions when a bull seemed to be trying to "herd" a cow or keep her from moving away. This pattern seems to be similar to the "twist" performed by courting mountain sheep rams (Geist 1971a).

Mounting sequences seen in September while herds were being attacked by wolves or approached by humans may have been due to a high level of excitement and the consequent physiological changes and perhaps to the close contact between bulls and cows. This contact would provide the bull with opportunities for detecting oestrous cows or might simply provide the necessary stimulus for mounting. Henshaw (1970) described

high frequency of breeding in reindeer during herding by man and discussed several factors, including the above, which may account for the increased breeding. Hinde (1966) mentioned several other examples of sexual behaviour appearing in irrelevant situations where there was an aggressive component (eg., after a mild disturbance).

Wilkinson (1971) reported that captive muskoxen are "reticent about their breeding activities" and few copulations in captive animals have been observed. Tener (1965) apparently observed only three successful matings (copulations) in the wild. Copulation is reportedly very swift but is usually preceded by several attempted mountings (D. Bellaar-Spruyt, pers. comm.).

The periods of heat or oestrus of seasonal breeders, such as the muskox, may be defined as "periods of proper psychological and physiological state, during which copulation is permitted.... When in heat, a female is in a psychological state that is distinctly different from her state during the rest of the cycle" (Nalbandov, 1964, p. 119).

Although virtually nothing is known of the behaviour or physiology of oestrous female muskoxen in the wild, observations made by J. Bourque (pers. comm.) at the muskox farm at Old Fort Chimo, Quebec, indicate that a cow stays in heat for a few hours, "shows a great desire for the male" and accepts the

male about every 30 minutes during that time. The herd bull drives an oestrous cow away from the others and drives away any approaching females. This behaviour is similar to that described for bison by McHugh (1958) and his term "tending-bond" seems appropriate for muskoxen.

Despite the numbers of muskoxen in the study area during the expected rutting season (eg. up to 50 females in 1959), and despite an increase in number of herds under observation, no copulations or sequences of mounting were observed during the four partial rutting seasons covered by this study. Although some manifestation of the rut was evident in males, no tending-bond behaviour was noted and the formation of harems did not occur. Active courtship by cows was not seen and on the few occasions when cows appeared somewhat receptive, mounting did not occur. All of these observations suggest that for the first half of the study at least, breeding did not occur in this population.

Unfortunately, it is not possible to make accurate comparisons of rutting behaviour between the four years of the study because of the differences in timing of observation periods during the four rutting seasons. Because different herds of different sizes and different sex ratios were observed for varying lengths of time and because only a few bulls in a herd (usually only the dominant bull) were involved in courtship interactions, and because most cows involved showed little

sign of receptivity, I felt that a breakdown of observations into number of interactions per animal per unit time would not be meaningful.

However, the change in completeness of rutting behaviour (i.e., the number of patterns performed in sequence) from 1968 to 1971 and the production of one or two calves in the study area in 1971 indicates a return to a breeding situation.

V. COMPARISON OF MUSKOX BEHAVIOUR PATTERNS WITH OTHER UNGULATES

The taxonomic and evolutionary relationships within the family Bovidae are not well known (Simpson 1945) and the relationships between many species, genera, and even tribes, in the subfamily Caprinae are uncertain. Geist (1966, 1971a) elaborated on this problem and discussed the significance of behaviour patterns to evolutionary relationships between the rupicaprid and caprid tribes.

Simpson (1945) placed muskoxen in a third tribe, Ovibovini, along with the little-known takin, *Budorcas* sp. (see Appendix VII). Earlier authors had considered the muskox to be closely related to the bison (eg. Seton, 1927). The taxonomy of the living and extinct members of the genus *Ovibos* was reviewed by Tener (1960, 1965) and Harington (1961).

Comparison of muskox behaviour patterns with those of other members of the subfamily eg. the caprids, *Capra* and *Ovis* (Hafez 1969, Geist 1971a), and the rupicaprids, *Oreamnos* and *Rupicapra* (Geist 1965, Krämer 1969) shows that few behaviour patterns are unique to the muskox. Comparison of muskox behaviour patterns with those of the bison, *Bison bison*, (McHugh 1958, Fuller 1960, Herrig and Haugen 1970) again shows many similarities although the bison is in a different subfamily, Bovinae.

The agonistic behaviour patterns of the muskoxen are similar to those seen throughout the family Bovidae. The charge and clash of the muskox resemble closely the caprid patterns (Schaffer 1968, Geist 1971a), although the muskox clash contains more components than most.

The broadside display is widespread among mammals and is common among the bovids. The head-tilt broadside display of the muskox is, for example, similar to that of the mountain goat and is almost identical to that described for the takin by Schaller (in press). The takins at the Bronx Zoo ... "commonly arch their neck far down with chin tucked in and ears retracted and, moving stiffly, present their broadside. The head is often slightly averted and snorts may be given" (Schaller, in press).

The pattern I have termed "gland-rubbing" is probably the most distinctive of all muskox behaviour patterns. Many other bovids have preorbital glands and rub them against the substrate or on conspecifics (cf. Geist 1971a) but to my knowledge, the muskox is the only bovid that commonly rubs the preorbital gland against part of its own body.

The courtship behaviour of muskoxen is also similar to that of many bovids. The initial elements of courtship are similar over a wide range of ruminants. The foreleg kick is seen in the subfamilies Caprinae and Antilopinae but

not in the Bovinae. Placing the head up over the rump of the female is not seen in many of the Caprinae. This pattern, seen in the muskox, is however,seen in the bison, immediately preceding mounting. The male mountain goat does rest his head on the female during mounting. The body contact with the female in the "moving-up-alongside" pattern is also somewhat unusual. Moving up alongside the female occurs in the chamois, for example, but without direct body contact. In the caprids also, body contact is usually restricted to nosing at the rear and actual mounting.

Body contact between adults in non-courtship situations is relatively common in muskoxen. Mutual "grooming" in the form of rubbing rear ends together is seen more often than many other forms of grooming. The well-known and unique defence formation of the muskox is also based on close contact between individuals in situations of disturbance or attack. This kind of close-contact, defence formation is rarely seen even in other social bovids living in herds.

FINAL DISCUSSION AND CONCLUSIONS

Ewer (1968, p. 1,2), in referring to modern ethological studies, observed that "structure, behaviour and mode of life form an integrated adaptive unity...of which no one component is comprehensible except in relation to the other two.... [They] are only partly comprehended if we do not add to them evolutionary history and relationships with other species."

The scope of this study has included some aspects of each of these five topics and this discussion is partially an attempt to demonstrate the ways in which they are so closely integrated.

Muskoxen are well adapted both structurally and behaviourally to the arctic environment. Tener (1965) discussed in detail some structural features of the muskox such as the wool coat, broad front hooves, the eye and the short limbs that are adaptations to the "harsh" arctic environment.

Behaviour patterns considered under maintenance behaviour also reflect the muskox mode of life. The locomotory patterns of the muskox are, with the exception of the gallop, slow. The usual slow movements of individuals and herds are

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

[illegible]

likely a method of conserving heat in winter (Tener, 1965) and, in summer, may help to prevent overheating.

The methods of feeding, like the snow cover itself, are variable, changing from the simple pushing aside of soft snow with the nose to pawing and head-dropping to break the thick wind-crusts.

Tener (1965) described how the general behaviour of muskox herds (i.e., their movements within feeding areas every few days) is well suited to range conditions of the arctic and helps to prevent over utilization of any one area. My observations in winter indicate that the cratering of feeding areas and the subsequent covering of unused vegetation by disturbed snow may prevent over utilization since muskoxen do not usually return to feed in disturbed areas (cf. Pruitt, 1969 for caribou).

In the Bathurst Island study area during winter muskoxen do not feed on exposed, windswept slopes, but rather along the broad valley floor where the snow cover is relatively deep but vegetation is comparatively lush. Below this deeper snow layer, at ground level, the vegetation is usually in an air space and may be much easier to utilize than vegetation frozen into a thin layer of compacted snow on a windblown slope.

Although in some areas winter and summer ranges can

be separated by 50 km or more (Tener 1965), in this study muskoxen were found to feed in the same areas in both summer and winter. The animals used the northern side of the valley in late winter and early summer, mid-valley in mid-summer and early winter and the southern side in late summer and the fall.

Since this study was the first to study the muskoxen of one area during an entire winter, much information on wintering muskoxen is still lacking. Until an expanded program of tagging is carried out, seasonal and yearly movements of muskoxen within and between known ranges and the possibility of movement between islands will remain poorly understood.

In discussing the "advantages" of herd formation, Tener (1965) included protection from wolves, "passing on" of knowledge of the environment through the association of old and young animals and ensuring contact of the sexes at the breeding season. Of these, protection from wolves may be the most important in this respect since many solitary species successfully accomplish such learning and contact of the sexes. Wynne-Edwards (1962) has suggested that there is no existing and generally accepted theory regarding the purpose of the herding habit in mammals which may simply be an alternative to solitary life.

The activity cycle of muskoxen takes the form of al-

ternating periods of feeding and resting-rumination lasting about 2½ hours each. Although individuals within a herd tend to have feeding periods of different lengths, their activity cycles are synchronized. This synchrony is likely a result of contagious behaviour occurring especially at the end of the resting phase of the cycle. The cycle with two daily peaks of activity present in ruminants in temperate regions would not be relevant to the arctic situation. Muskox herds continue on the alternating cycle through the 24 hours of sunlight on summer days and through the 24 hours of starlight on early to mid-winter days. Information on winter activity cycles is lacking for December and January and the activity cycles of the large groups observed in February were not synchronized.

The social organization of a species is an adaptable system which can vary with changing environmental circumstances. Vibe (1958, 1967) showed that the age structure and sex composition of muskox herds in Greenland changed from the usual situation following heavy winter mortality caused by a heavy snowfall and ice-crusting. No calves, few yearlings and an unbalanced sex ratio in favour of bulls were recorded.

The mortality in the Bathurst Island population during the winter of 1967-68 and previous years may have been due to a combination of similar factors including long winters, relatively deep snow and short summer growing seasons.

Tener (1965) suggested that the quality of winter forage restricts muskox reproduction. Reductions in quality and quantity of vegetation, which may result from a short growing season and other factors, in combination with decreased accessibility of food due to snow conditions, probably affect the nutritional state of muskoxen in winter.

That nutritional factors can limit reproduction is well known (see Tener 1965 for review). If domestic mammals are fed on diets deficient in any essential factor such as vitamins, minerals or protein, reproduction can be interfered with resulting in a cessation of breeding (Sadleir 1969). Although starvation is rare in wild mammals, "it is more than possible that seasonal deficiencies in certain dietary items may affect their reproduction"(Sadleir 1969, p. 144).

The ways in which the nutritional state of muskoxen might affect production of calves include failure of cows to come into heat or bulls into rutting condition, a serious loss of weight resulting in loss or resorption of the foetus (cf. Geist 1971b) and birth of calves of insufficient size and weight to survive the crucial time following birth.

There was no evidence during this study of predation or late winter mortality of newborn calves.

Although the likelihood of cows failing to come into full oestrus condition is small, their nutritional state may

have been poor enough to prevent the behavioural manifestations of oestrus. The lack of normal rutting behaviour in bulls may also have been related to nutrition. The level of nutrition available may be the major ecological factor affecting the rut (Sadleir 1969). The quality of the vegetation in the study area in summer at the time of rut may not be as important as the quality and quantity in late winter since there may be a delay between the presence of an environmental variable and its effect on reproduction (Sadleir 1969). Unfortunately no data are available on quality of the vegetation for the study area.

Failure of cows to reach an oestrous condition would help account for the very low frequency of rutting behaviour seen during the expected rutting season. The observed low frequency of agonistic or aggressive behaviours among bulls of the herd would be expected if both cows and bulls were not in prime breeding condition.

Wilkinson (1971) reported that "strutting" (which seems to be equivalent to the display I call the head-tilt) increases in frequency during the rutting season of domesticated muskoxen in Alaska. Apparently, it is seldom seen at other times of the year. Oeming's (1965) brief report and Teal's (1959) comments also indicate that rutting dominant bulls display frequently and exhibit a much higher level of aggressive behaviour during rut. Numerous other reports

in the literature suggest that bulls during the rut are more dangerous and more likely to attack other species and even inanimate objects (see Hone 1934).

Tener (1965, p. 73) noted that fighting between bulls occurred outside the rutting season but did not consider these "contests...to be motivated in the same way as contests in the breeding season." Unfortunately, Tener seems to lump simple butting interactions and the more elaborate fights or clashes under the one category of "fighting," thus making his interpretation of different motivations difficult to evaluate.

My own observations show that displays and aggressive behaviours including butts and charges occurred in most seasons and were not primarily related to the presence of cows and the breeding season. Rather, these behaviour patterns are an integral part of the social dominance system which seems to exist year-round. The kind of motivation behind the display of these patterns is probably constant but is certainly influenced and perhaps strengthened by changing circumstances during the rut. However, no obvious increase in agonistic behaviour was observed during the rutting seasons of this study though all four clashes observed occurred at this time.

The observed low level of aggressive behaviours in an animal which reportedly shows an increased level of aggression during the rut probably accounts for the equal sex ratio

observed. Presumably, in the "normal" situation, young or subordinate older bulls (which are probably capable of breeding) are driven from a herd containing oestrous cows by the aggressive dominant bull. In my study population these bulls remained in the herds throughout the rutting season.

The role of solitary bulls in the social organization of muskoxen is not well known. Although most solitary bulls seen during this study were adult, two solitary subadult bulls were seen. Lent (1971) has discussed the need for further information on the relationship of these bulls to breeding and the herd formation.

The social structure of a muskox herd is an open system in which strange individuals can join a herd (except, presumably, during the rut) with a minimum of agonistic interaction taking place. Herds joined frequently, often with little or no overt interaction. Wilkinson (1972) suggested that the open nature of muskox herds serves two functions: (1) to prevent inbreeding which might result if a single bull dominated breeding within a given herd or area for many years, and (2) to allow solitary sub-adult and adult males to form temporary single-sex groups, thus decreasing the likelihood of predation. Given the mixing of herds that occurs both before, during, and after the rut, as well as the recombinations of herds that occur as the large winter aggregations are formed

and disperse, it is certainly highly unlikely that inbreeding could become a problem in muskox herds. However, the openness of herds is of far greater importance in terms of allowing solitary individuals to join not only single-sex herds but mixed herds as well and permitting the formation of large herds in early winter.

Although muskox herds can be classified as open social units, there is a fairly high frequency of agonistic behaviour within herds. This seems reasonable in view of the mixing that does occur. Individual muskoxen, unlike mountain sheep (Geist, 1971a) apparently cannot determine the dominance rank of other muskoxen by physical characteristics; some interaction must occur to sort out the dominance relationship. There appears to be a social class dominance (which may be more easily recognized) as well as the linear dominance hierarchy within a social class (which depends on frequent interactions and individual recognition).

The agonistic behaviour patterns of butting and charging apparently serve to determine dominance relationships between most bulls. Displacements from feeding craters reflect the established dominance hierarchy. The expressive behaviours, the head-tilt and gland-rubbing displays, are methods of expressing dominance and can serve as threat displays. Use of these latter patterns reduces the probability of serious fighting and injury by decreasing the element of surprise and allowing the second individual to flee, modify

his behaviour or counter-display. Only in situations where the individuals are strangers or well-matched in terms of strength, and only after counter-displaying, do clashing fights occur.

The clash in muskoxen, as in the Caprini, is a ritualized fight. The bull muskox is well equipped for absorbing the shock of a head-on blow. Although a misplaced head-on blow can cause severe damage (Tener 1965), it is the pushing and circling contest following the stereotyped ramming which is potentially most dangerous. If the combatants cannot keep the head-to-head orientation, jabbing and hooking with the sharp horns can result in serious injury.

The muskox clash, with its ramming and pushing component, together with the preceding broadside display, fit into Geist's (1966) "tree" of the evolutionary development of fighting in bovids somewhere between the broadside-displaying, head-pushing bison and the horn-displaying, ramming mountain sheep.

The close relationship between dominance and leadership is an important element in the social organization of muskoxen. The relative stability of herds together with the linear dominance hierarchy established through frequent agonistic encounters between individuals, results in the more-than-temporary overall dominance of one individual. This dominant

individual, through his behaviour, influences the rest of the herd. His influence on the herd, in herd movements, stampedes and general behaviour under disturbed conditions, such as attack by wolves, is connected with contagious behaviour and is a basic part of leadership. The dominant animal (eg., LB in herd 69-A-4) leads the herd in movements and directs the herd through his influence in other situations and dominates all of the herd in agonistic encounters. In the literature (see Hone, 1934; Tener, 1965), the terms "lead" and "dominant" bull are often used synonymously. The generality of this conclusion is also supported by Pedersen's (1958) observations of dominant bulls influencing herd movements.

In those species where the animals separate into all male bands and female-young bands, such as bison and mountain sheep, the relationship between dominance and leadership is not as clear. In bison, a few cows "lead" the mixed herds most of the time and a large bull usually leads the bull groups (McHugh, 1958). In mountain sheep, dominant males lead the all male bands but certain females lead the mixed groups which contain young rams dominant to the females (Geist, 1971a).

Courtship in muskoxen, as well as displaying, is the prerogative of the dominant bulls (cf. Geist, 1971a for sheep). Much of the rutting activity observed in this study

was performed by bulls that I recognized as dominant or "lead" bulls.

The presence of a linear dominance hierarchy and the displacement of individuals from feeding craters in winter suggests that social behaviour may be an important factor in limiting reproduction in years with poor winter conditions. However, information on certain of the conditions proposed by Watson and Moss (1970) as being necessary to demonstrate that behaviour limits breeding populations, is lacking.

Because cows are the lowest ranking adults in the dominance hierarchy, are displaced relatively more often than bulls, and use new areas for feeding more often than do displaced bulls, there is a possibility of the cows being the first to be affected by the increased energy demands probably associated with deep or thick-crusted snow.

Espmark's (1964) studies on wintering Reindeer showed that cows, which retain their antlers longer than bulls, are higher ranked in the winter dominance hierarchy and thus they and their calves are not so often displaced from feeding craters. The relative dominance of muskox cows accompanied by calves is unknown.

Tener (1965) and Bos (1967) described play in calves, noted that play is unusual in adult muskoxen, and suggested that the milling about, running and chasing by all animals in

a herd was play activity. Similarly, I interpret the chasing and incomplete, irregular butting interactions between cows and bulls observed in herds in early summer as play. Other observations such as the cow performing incomplete clashing patterns and leaping about on a snowbank, and the whirling about and splashing in summer ponds also appear to be best described as play. A suitable definition of the verb to play is "to move about swiftly with a lively or capricious motion, especially with irregular manner"(The Oxford English Dictionary, 1961). The low frequency of occurrence and the absence of biting insects and external parasites preclude the usual explanations for such activities.

Of the relationships between muskoxen and other species, the most important are those involving the wolf and man. The defence pattern of crowding together in a line or circle is well known to be relatively effective against attacking wolves, though my observations indicate that it is certainly not always effective.

Wolves expended more time and apparently more energy in killing muskoxen than in killing caribou (S. D. MacDonald, pers. comm.) and are more persistent in their attacks on muskoxen than southern wolves are in attacking moose, Alces alces (Mech, 1970). It is unlikely that predation by wolves has a significant effect on muskox populations.

Disturbance by humans, though having results similar

to disturbance by wolves, may be of greater importance because of the increasing frequency of muskox-human contacts. Geist (1971b, p. 420) stated that the effects of disturbance, including alienation from available habitat, are likely to be most severe in those "social species in which individuals have high life expectancies, low reproductive rates, a retention rather than dispersal of juveniles, and which inhabit widely dispersed patches of stable habitat." The muskox fulfills all of the above conditions and further research on the effect of various kinds of disturbance is necessary.

A continued monitoring of the Bathurst Island population over several years is desirable in order to test the tentative suggestion that the observed social organization and lack of breeding may be related to changing environmental conditions. A study of behaviour in the same population when oestrous cows are known to be present may provide much useful information on the role of the dominant male in rutting herds and could clarify the reproductive and social status of solitary bulls.

The role of calves in the social organization of the herd and their effect on herd behaviour, for example during winter, during storms and during various sorts of disturbance, would be an appropriate problem for further research.

The continuing study of muskox productivity on Devon

Island (Hubert, 1972) will undoubtedly answer many questions concerning muskox range, nutrition and feeding habits during winter.

There is a great deal yet to be learned about the muskox. Although present information is still an inadequate base for proper management programs, it is to be hoped that the results of the present and continuing research projects will be considered fully when decisions are made concerning the muskox and its environment.

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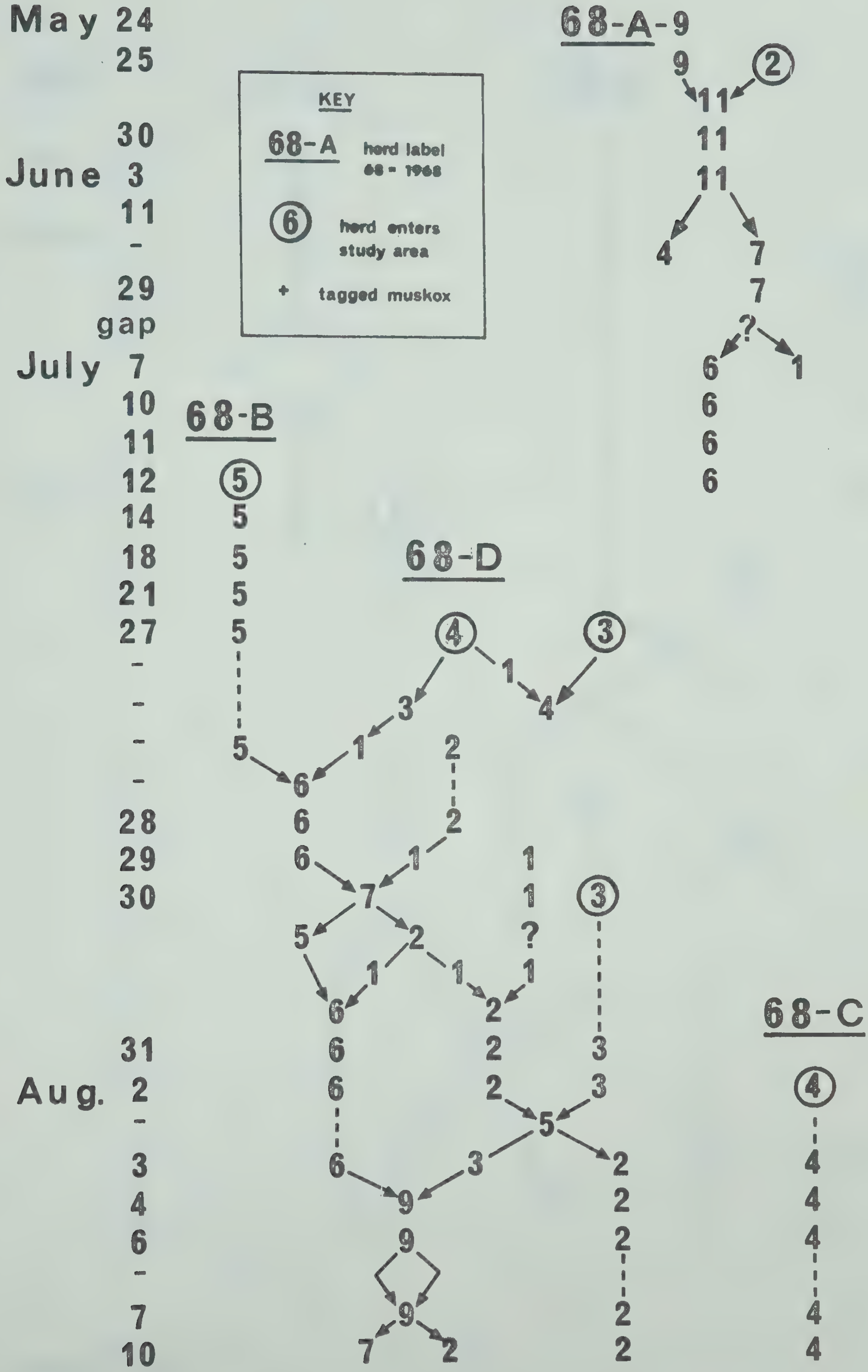
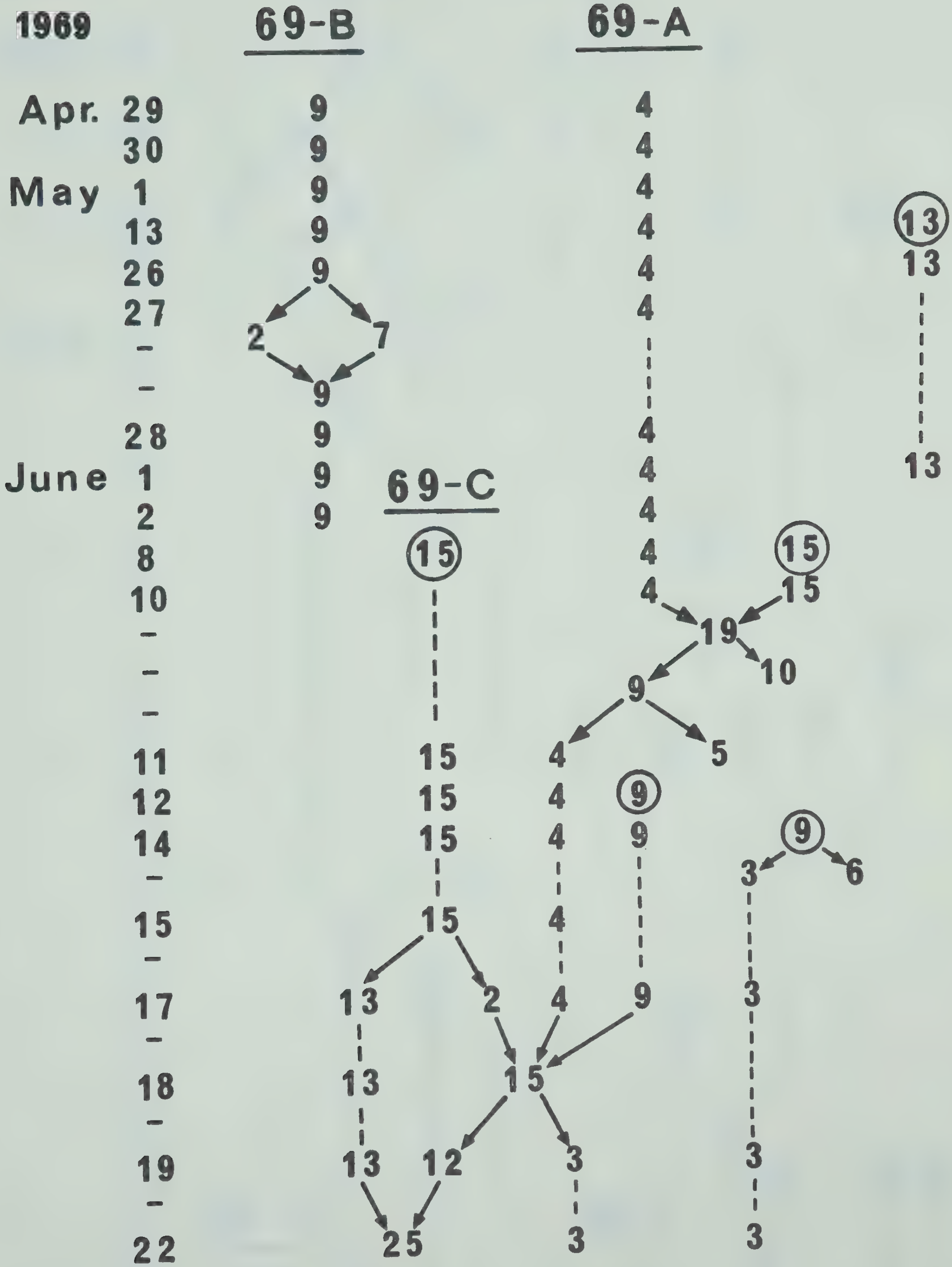
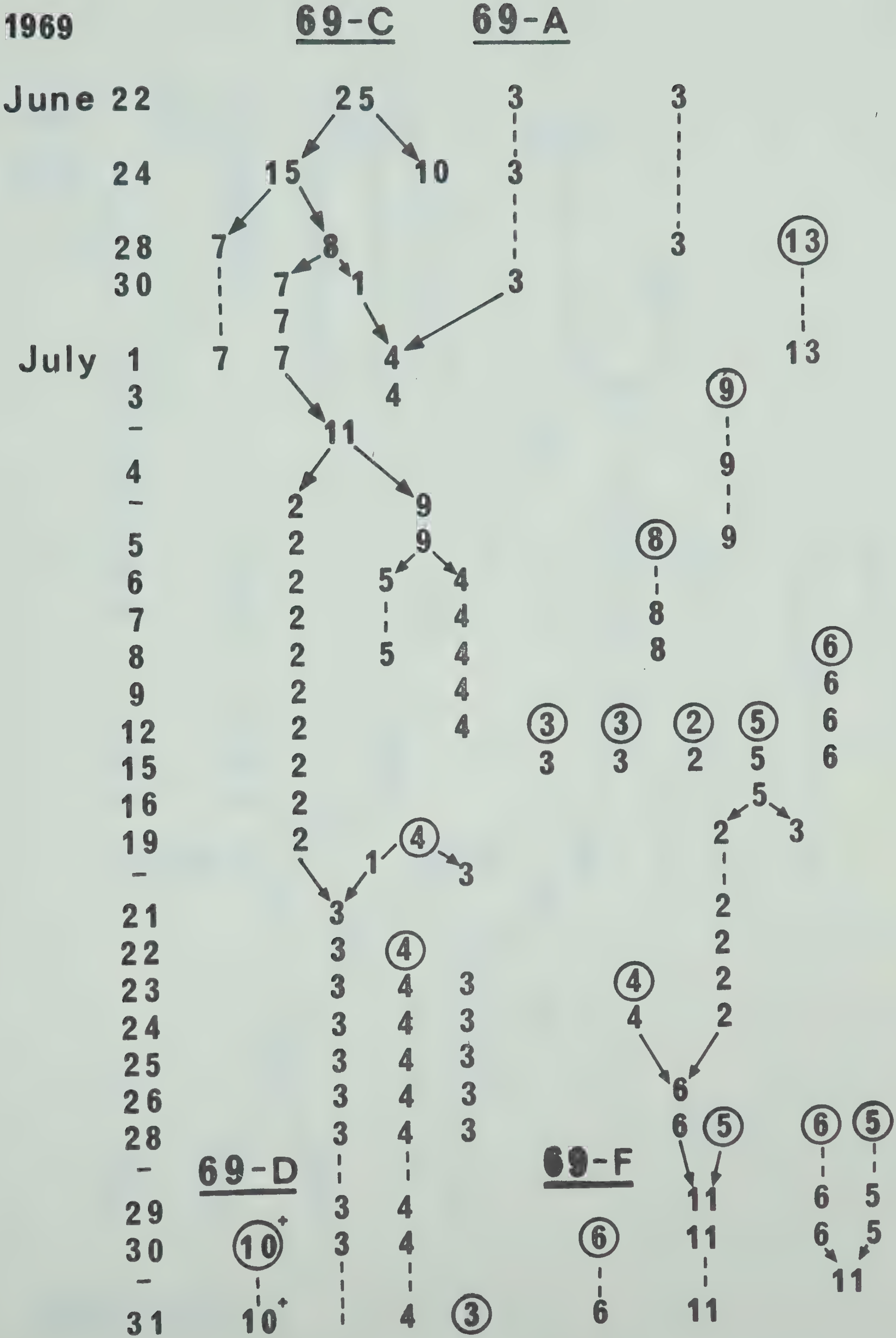
APPENDIX I Flow diagrams of herds in the study area showing joining, mixing and splitting of the herds.

Part 1	1968,	May - August
Part 2	1969,	April - August
Part 3	1970,	April - June
Part 4	1970,	August - November
Part 5	1971,	August - October

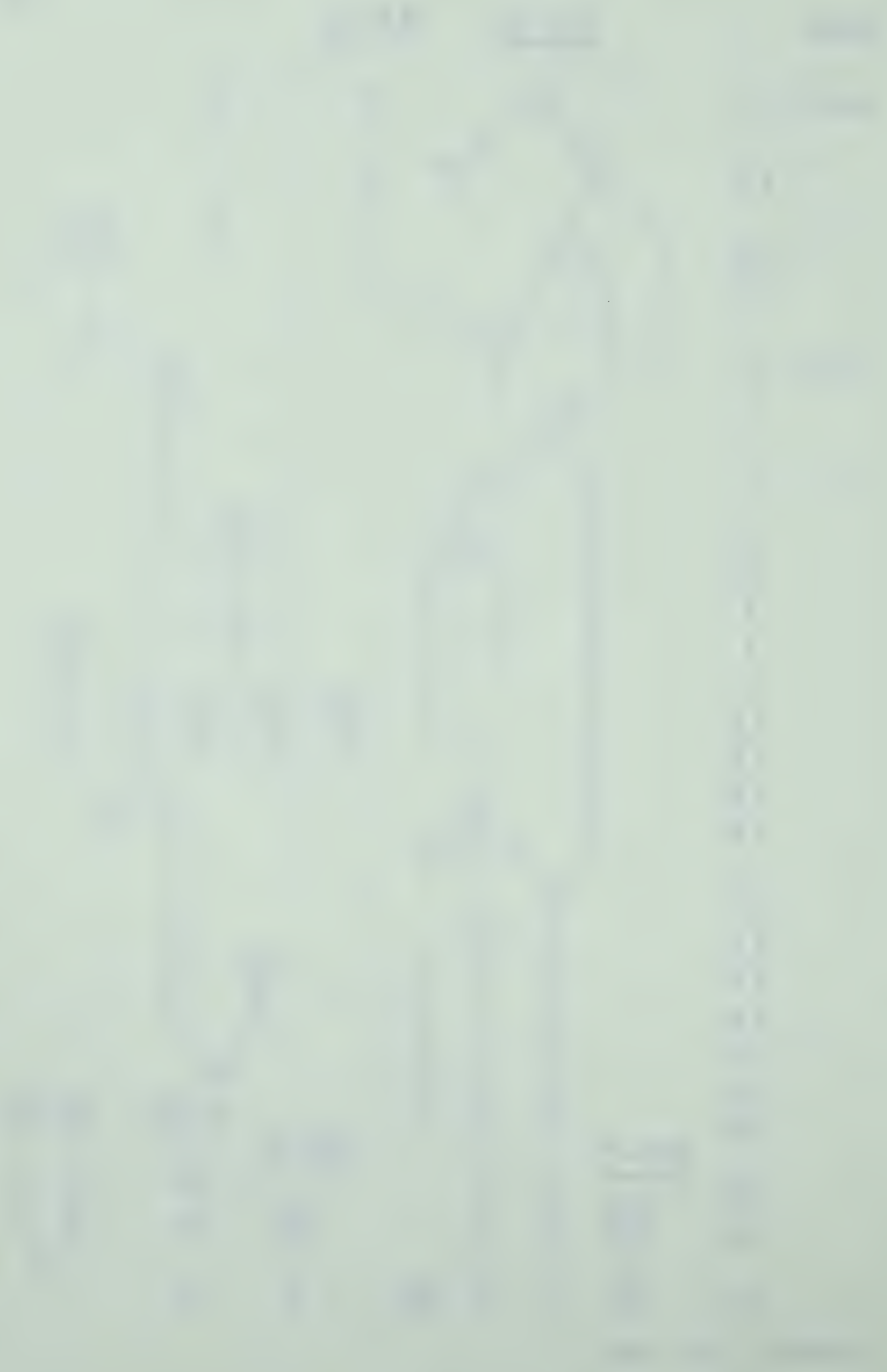


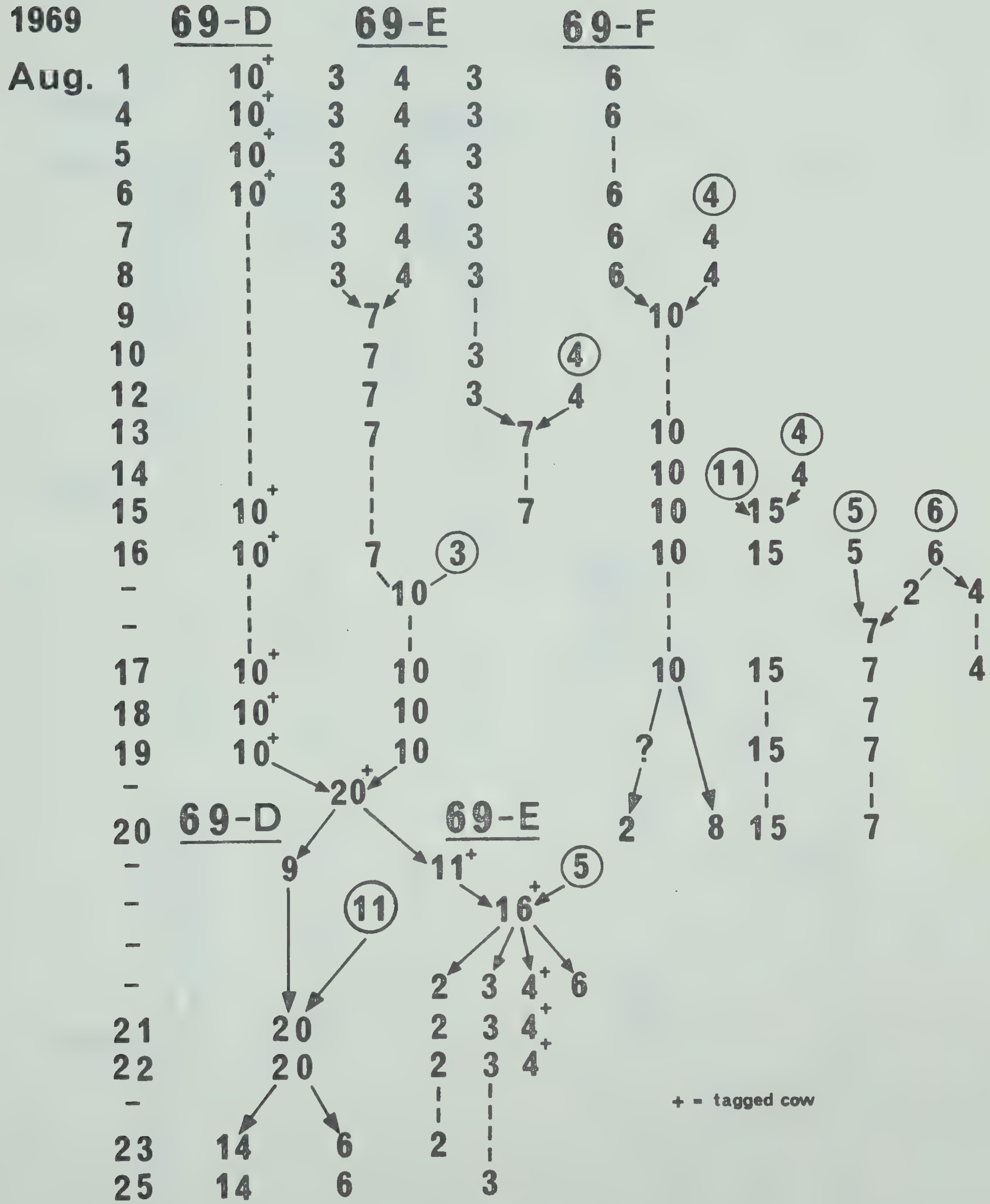
APPENDIX I, part 1


1969
69-B
69-A
69-C
Apr. 29
30
May 1
13
26
27
28
June 1
2
8
10
11
12
14
15
17
18
19
22



APPENDIX I, part 2 (cont.)





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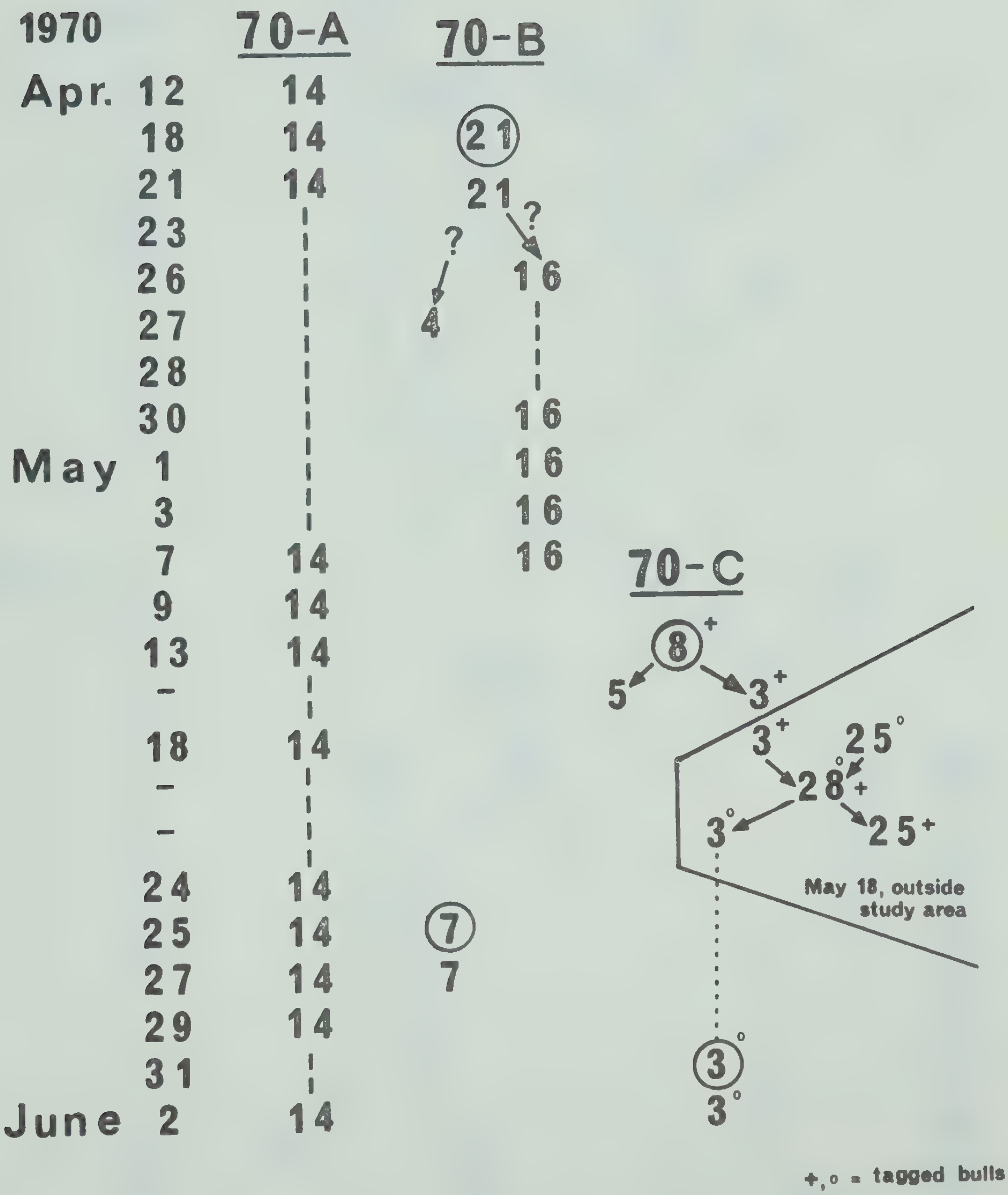
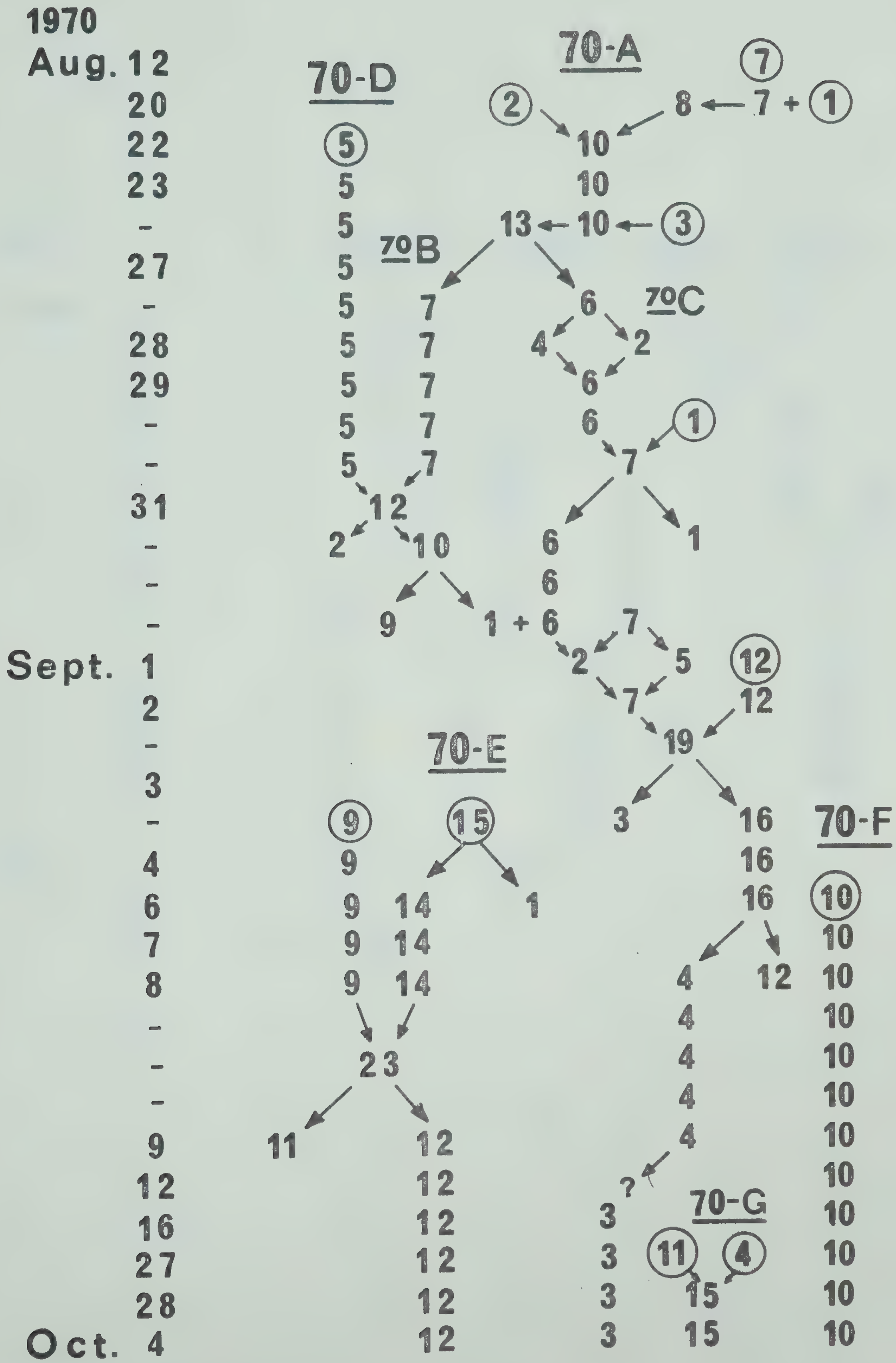
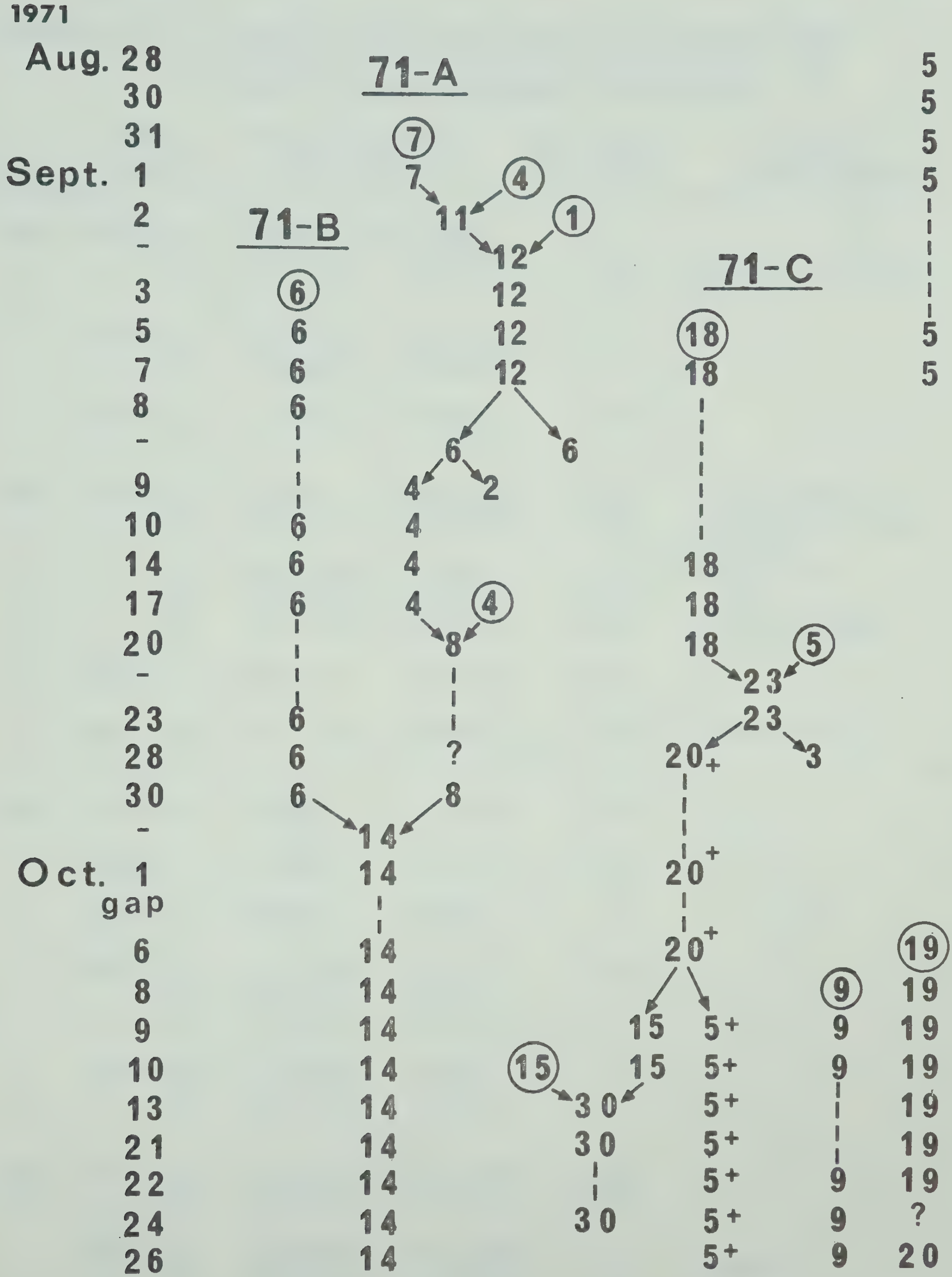


APPENDIX I, part 3


1970
Aug. 12
20
22
23
27
28
29
31
Sept. 1
2
3
4
6
7
8
9
12
16
27
28
Oct. 4
70-A
70B
70C
70-D
70-E
70-F
70-G

1970												
			70-E			70-C		70-G			70-F	
Oct. 5			12			3		15		10		
7			12			3			25			
9			12			3						
10			12			3		5		20		
12			12		8		8			20		
17			12		8		8			20		11
22			12		8		8				31	
23					8		8				31	
–		8		4	8		8				31	
24		8		4		16					31	
28		8		4							31	
29		8		4		10		6			31	
30		8		4		10					31	
1		8		4		10					31	
Nov. 5		8			14							
11		8			14							
14	3		5									
–			5									
18			5									

APPENDIX I, part 4 (cont.)


1971
Aug. 28
30
31
Sept. 1
2
3
5
7
8
9
10
14
17
20
23
28
30
Oct. 1
gap
6
8
9
10
13
21
22
24
26
71-A
71-B
71-C

+ = tagged bull

APPENDIX II The size and sex ratio of the major herds studied, with dates of observations and list of known or tagged individuals.

Year	Herd Label*	Time Period of Observations	Sex-Ratio Bull:Cow	Known Individuals
1968	68-A-11	25 May - 11 June		
	- 7	11 June - 29 June	5:2	CB,FB,LB,TB,YB, WC,TC.
	68-B- 5	12 July - 27 July	4:1	
	- 9	3 Aug. - 7 Aug.		
	68-C- 4	2 Aug. - 13 Aug.	4:0	
1969	69-A- 4	29 Apr. - 17 June	3:1	LB,1B,2B,C.
	-15	17 June - 18 June	6:9	LB,1B,2B,C,YB, HB,AB.
	- 3	18 June - 1 July	3:0	LB,1B,2B.
	- 2	4 July - 19 July	1:1	LB,C.
	- 4	6 July - 12 July	4:0	1B,2B,YB,HB.
	69-B- 9	29 Apr. - 2 June	8:1	
	69-D-10	30 July - 19 Aug.	0:10	C#69-10,GC.
1970	70-M-14	12 Apr. - 2 June	7:7	
	70-B- 7	27 Aug. - 29 Aug.	4:3	
	70-D- 5	22 Aug. - 29 Aug.		
	70-E-12	9 Sept. - 23 Oct.	4:8	
	- 8	23 Oct. - 11 Nov.		
	- 5	14 Nov. - 18 Nov.		
	70-F-10	6 Sept. - 5 Oct.		
	-31	17 Oct. - 1 Nov.		
1971	71-A- 6	3 Sept. - 30 Sept.	1:5	
	-14	30 Sept. - 26 Oct.	8:6	
	71-C-18	5 Sept. - 20 Sept.		
	-20	28 Sept. - 8 Oct.	6:14	B#71-4.

* see Appendix I.

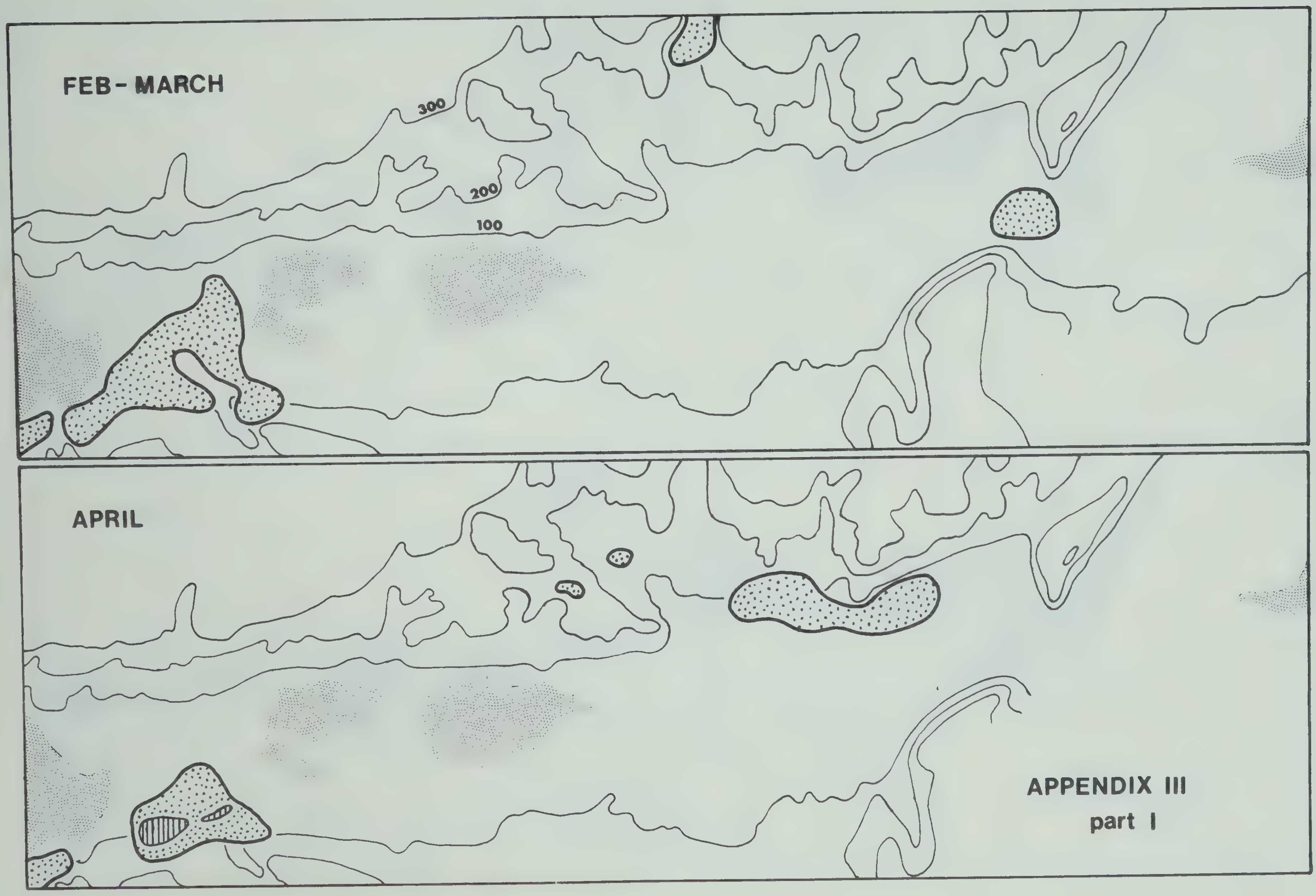
APPENDIX III Seasonal distribution of muskoxen in the study area.

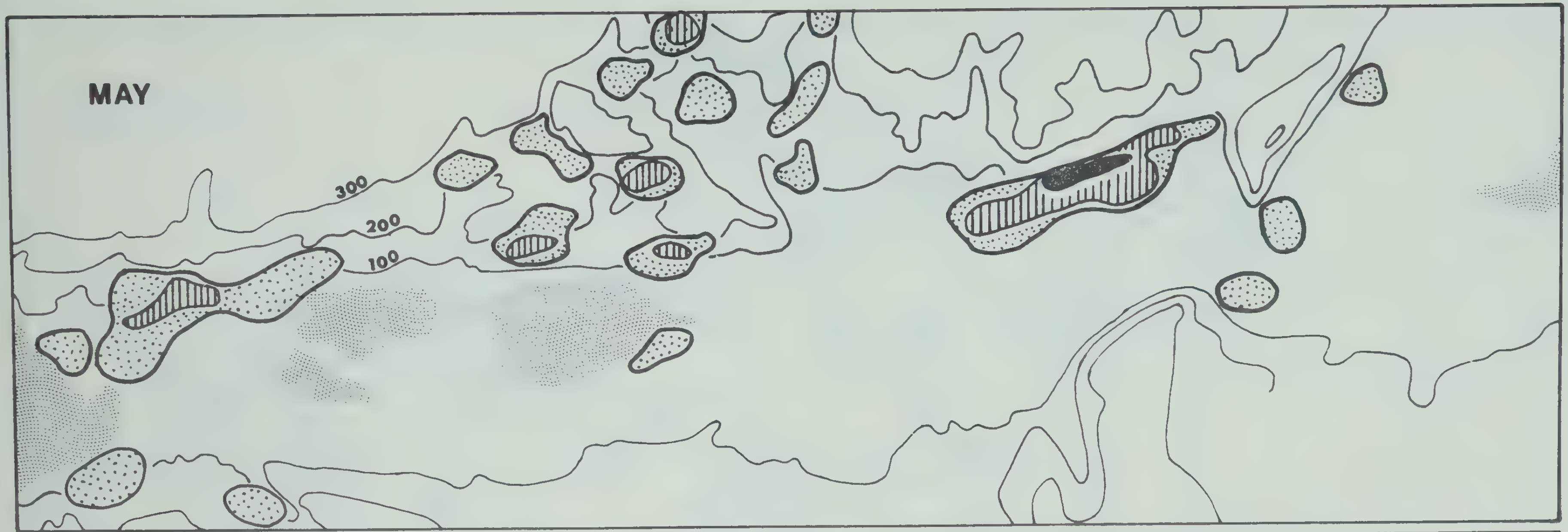
Part 1	February - April
Part 2	May - June
Part 3	July - August
Part 4	September - November
Part 5	The feeding areas used by herds 69-A-4, 70-E and 70-F.

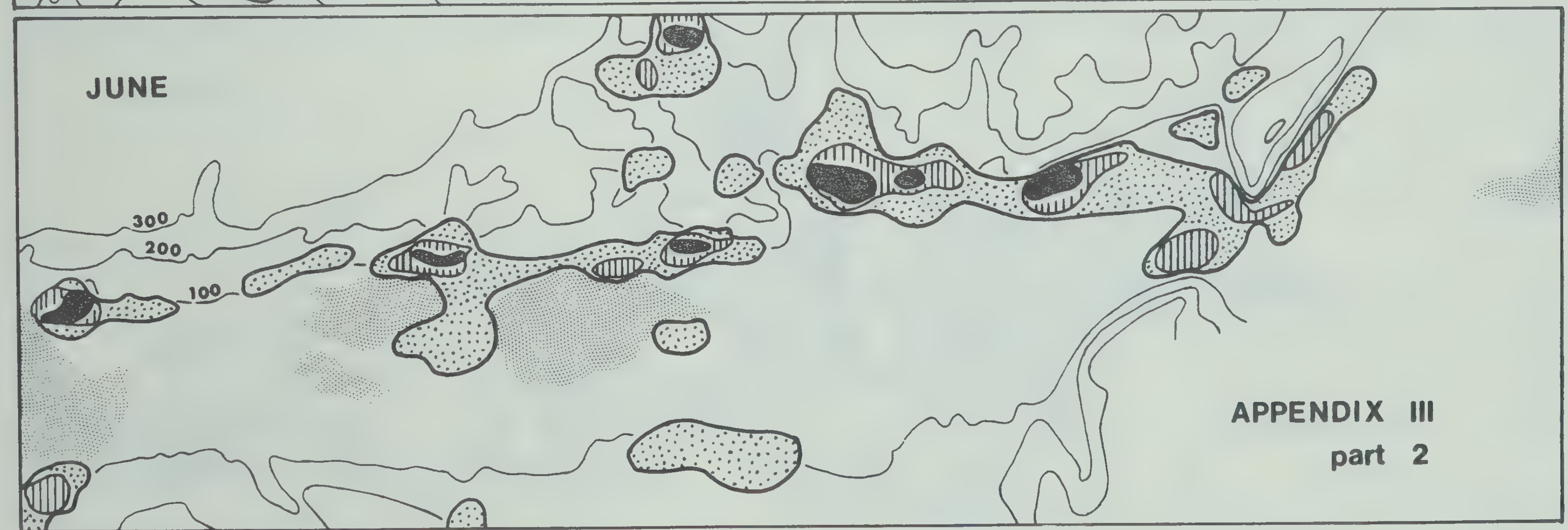
Feeding areas used in one of the four years only,

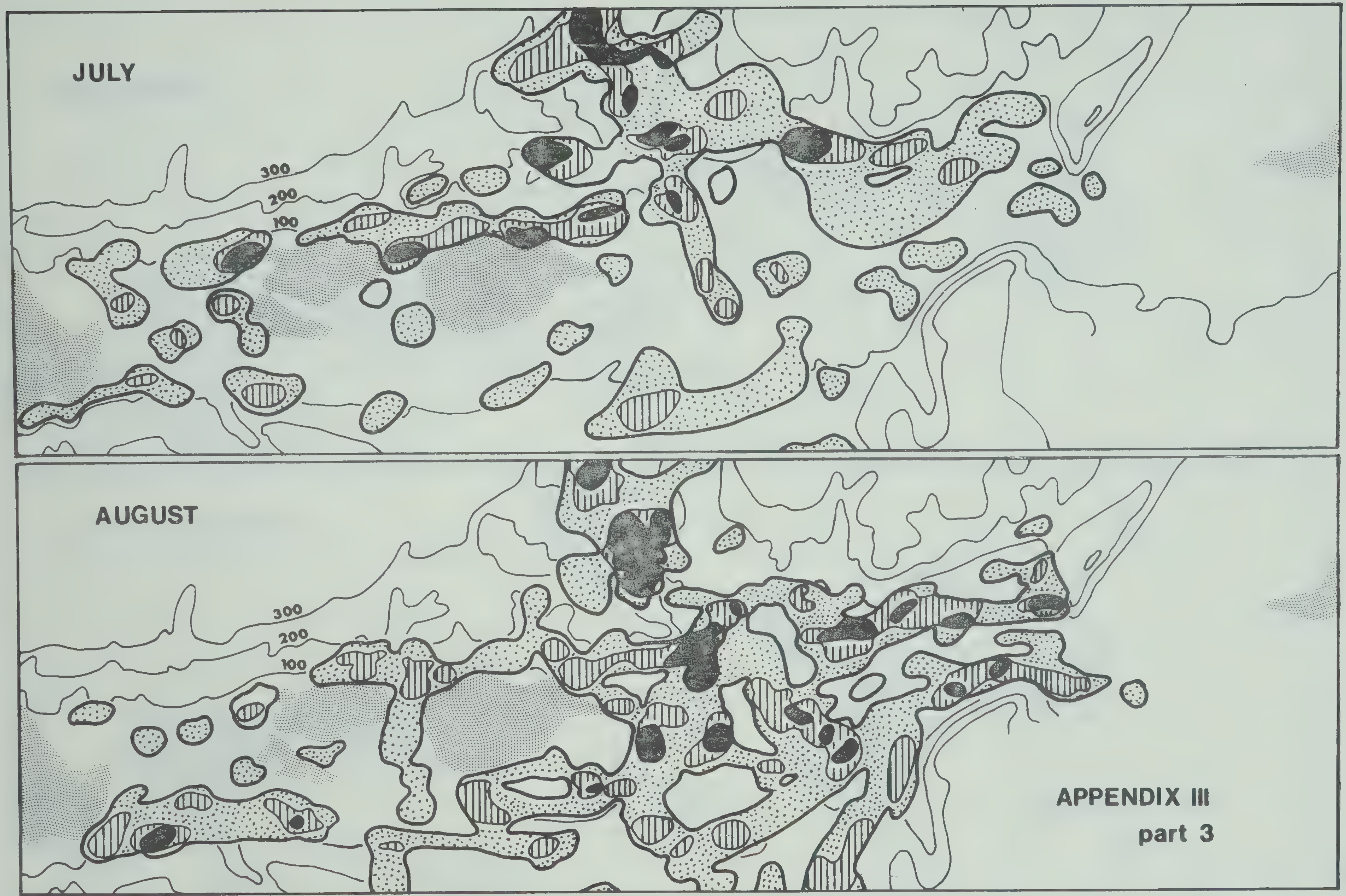
Feeding areas used in two of the four years,

Feeding areas used in three or four years.

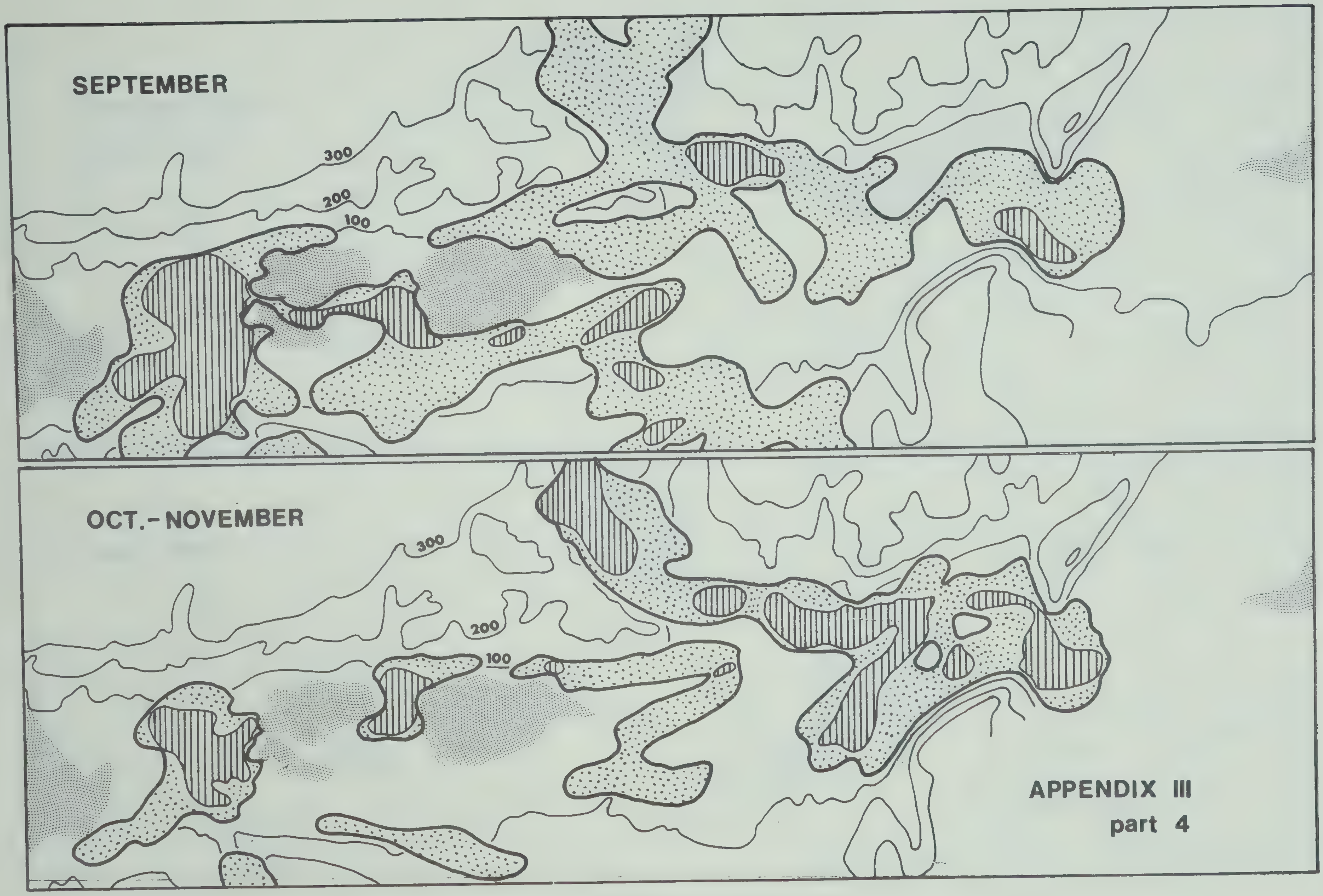

FEB - MARCH
300
200
100
APRIL
APPENDIX III
part I

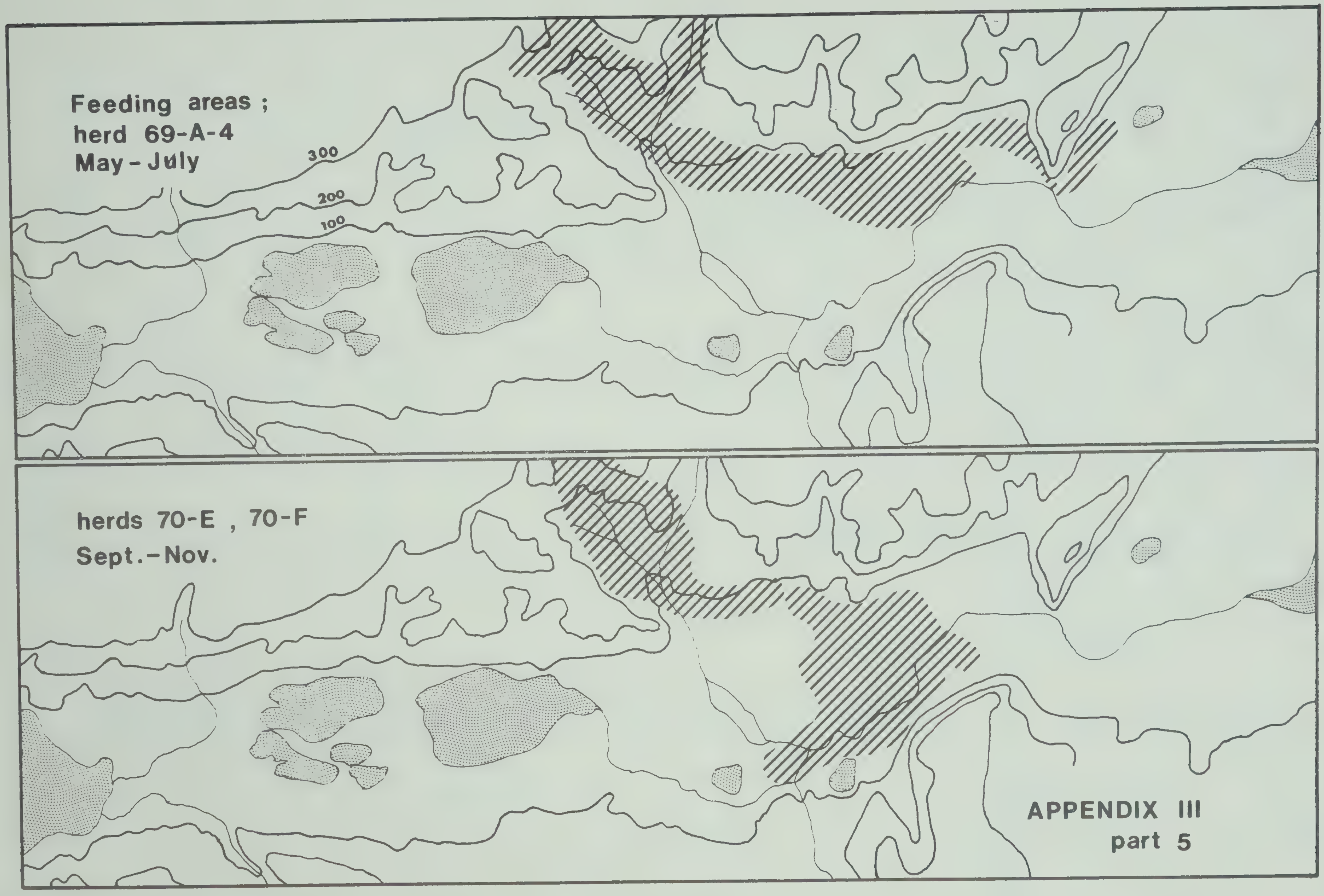

MAY
300
200
100


JUNE
300
200
100
APPENDIX III
part 2



APPENDIX III
part 3


SEPTEMBER
300
200
100
OCT.-NOVEMBER
300
200
100
APPENDIX III
part 4



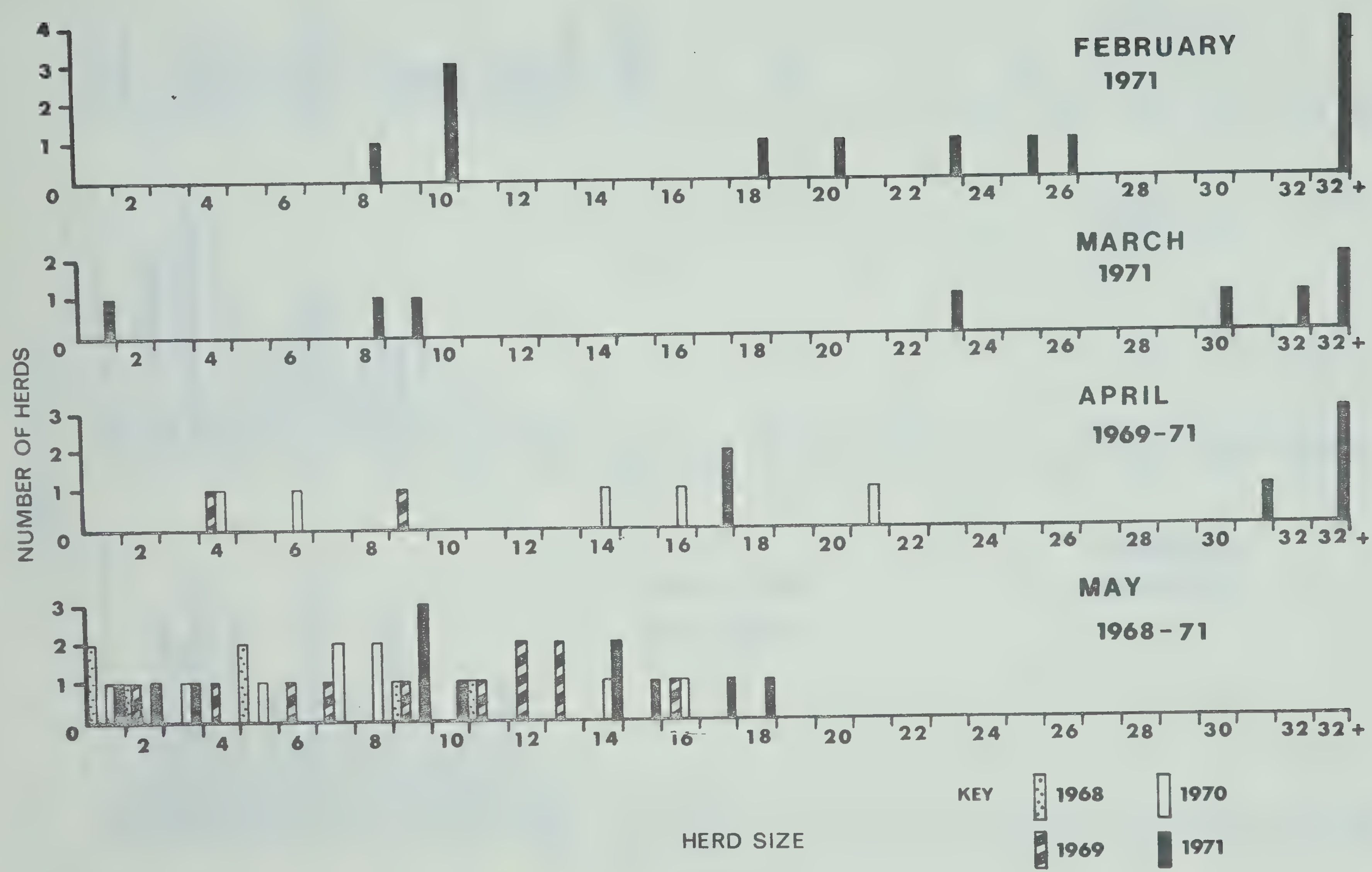
APPENDIX III
part 5

APPENDIX IV Herd size frequencies in the study area for each month of the study.

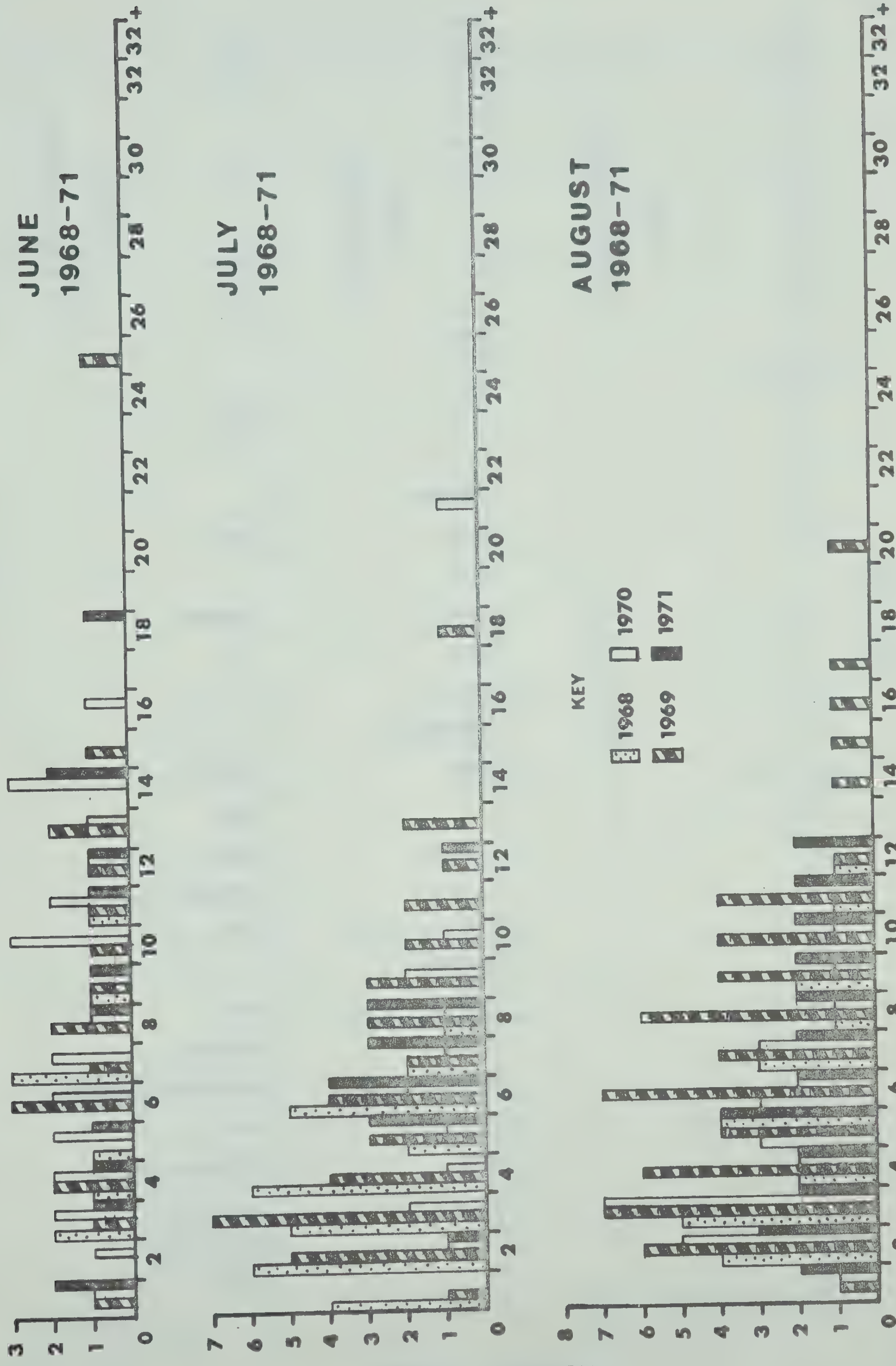
Part 1 February - May

Part 2 June - August

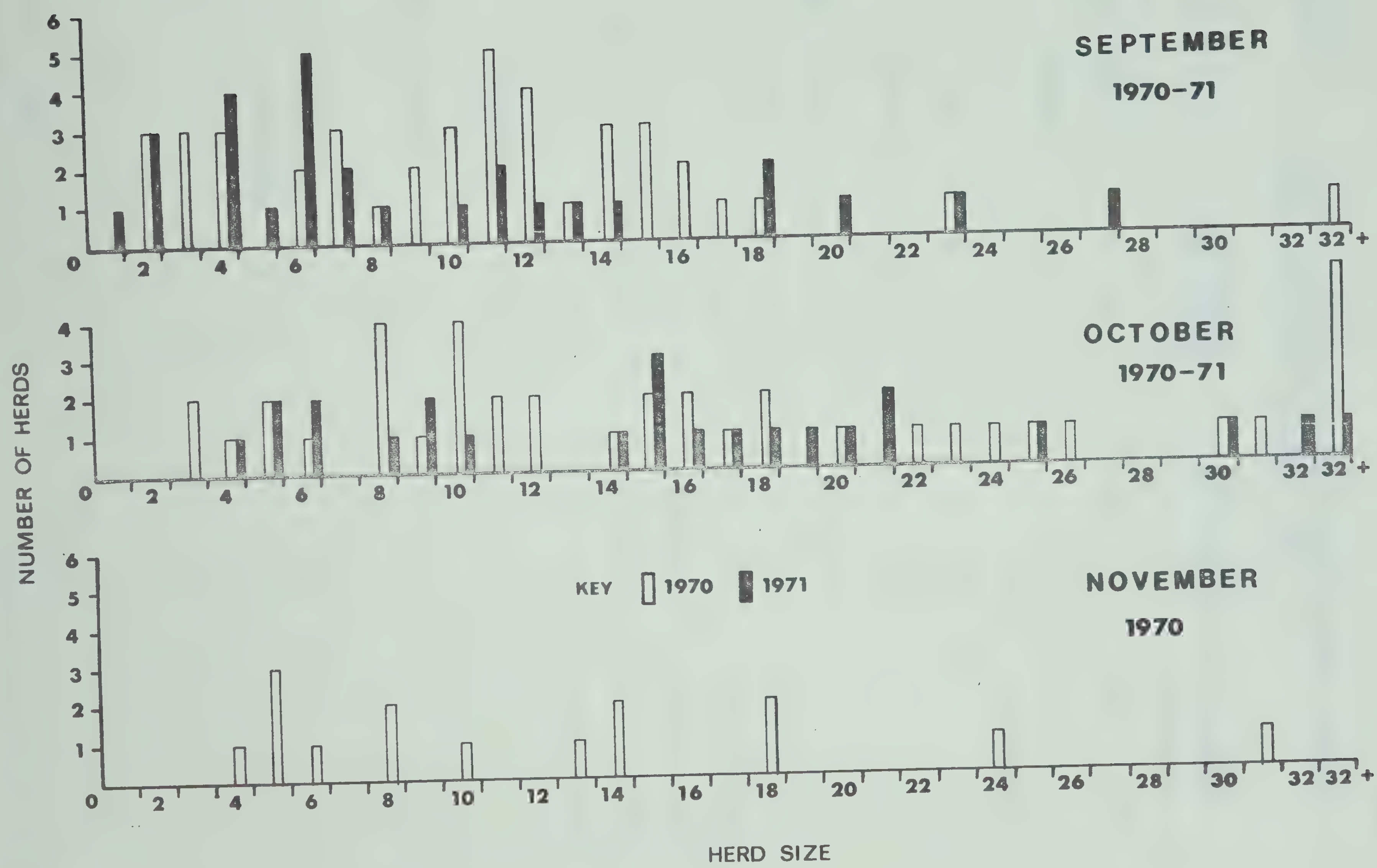
Part 3 September - November



APPENDIX IV, part 1



APPENDIX IV, part 2



APPENDIX IV, part 3

APPENDIX V List of subadult bulls seen in the study area, May 1968 to May 1971.

Year	Month	Estimated Age (Years)	Herd Size (or label)	Remarks
1968	May	3 - 4	68-A- 7	bull = "YB"
	June	5	5	
		3	5	(same herd)
	July	4	6	
	August	3 - 4	3	
1969	May	4 - 5	69-B- 9	
	June	4	6	
		5	6	(same herd)
		4	69-C-15	bull = "AB"
		3	69-A- 9	bull = "HB"
		4	" " "	bull = "YB"
	August	4	6	
1970	April	4	70-A-14	
		5	" " "	
	May	4	8	
	September	4 - 5	70-E-15	
		5 - 5	" " "	
		4 - 5	70-F-10	
		4 - 5	" " "	
1971	May	4 - 5	14	

APPENDIX VI List of single sex herds seen in the study area, May 1968 to October 1971.

Year	Month	Herd Sizes
Bull herds		
1968	May	2
	July	4
	August	4
1969	May	2
	June	3,3
	July	2,2,4,4,5
	August	2,2,3,4,4, 6,7
1970	May	5,5,8
	August	2,2,3,3
	September	3,7
1971	September	8
	October	5
Cow herds		
1969	July	3,4
	August	5,10
1970	August	4

APPENDIX VII. Notes on the Takin (<u>Budorcas</u>)

There is little information available on the biology of the takin (<u>Budorcas</u> sp.). Native to the mountainous regions of southern China and Bhutan, takins live in herds which move between high and lower elevations according to the season. Herds are larger in summer than in winter reaching a maximum of 100 individuals (Wallace, 1913). Herds are led by old males which have the largest horns. Following the rutting season in late July and early August, cows and young bulls live together in mixed herds. Old bulls are often solitary (Allen, 1940). Calves are born in March or April and follow the mother within three days of birth. Takins carry the head low and walk with a slow, lumbering gait (Wallace, 1913). However, like the muskox, they are extremely agile and can move very quickly when necessary. Herds are relatively local in habits and wander little from certain areas (Wallace, 1913). Takin bulls are larger than the cows and have a reddish tinge around the neck. The pelage colour differs in the subspecies with either a dark dorsal stripe or a buff saddle present on the back (Estes, 1959, Wallace, 1913). No pedal or preorbital glands are present (Allen, 1940). The horn bases are similar to those of the muskox but are less massive. They curve up, out and back rather than down, out and up as in the muskox. The orbits

protrude out beyond the horns (Allen, 1940) and there is a slight hump at the shoulder (Estes, 1959).

Although little is known of Takin behaviour in the wild, some behavioural notes are available. Butting between bulls is reported by Wallace (1913) and Estes (1959) described a threat display performed by a captive calf towards two Bos calves. The head was held out, low and rigid with the neck horizontal while the animal advanced. The calf made hooking motions with its hornless head and butted briefly with the other calves. Horning of trees was reported to be extensive in certain areas frequented by takin (Cooper, 1923). Schaller (in press) described a broadside display seen commonly in the takin at the Bronx Zoo.